The Origin of Sex through Cumulative Integration, and the Relation of Sexuality to the Genesis of Species.

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General Considerations.

A careful survey of the living world leads to the conclusion that sexuality has been, in all probability, one of the many results of the operation of the forces of evolution. A further examination of the evidence discloses the fact that sexuality has arisen very gradually and only through an extensive series of very gentle progressive and successive steps. These steps seem to have had a definite sequence and to have been accompanied by such a gradual complication of means, that it seems highly probable, indeed certain, that in many instances, a given higher grade of sexuality has grown out of the preceding one. This serial superimposition of means to serve apparently more advantageous ends proceeds according to fixed rules or laws, apparently determined by the already attained structural complication and physiological activities of organisms, and in conformity with the controlling conditions offered by their surroundings.

A still further examination of the data of sexuality leads to the conclusion that the methods of it which may be observed in the vegetable and animal worlds have proceeded along two parallel but distinct lines of progress. Both have ended in the achievement of the same result, namely, viviparity or the production of offspring in an advanced state of development, before the latter is set free from the parent to begin an independent existence for itself. An acorn is as truly a product of viviparous development as an infant human being. The elaborate process of organic evolution through which it has been possible to develop the one, is just as wonderful as in the case of the other.

The end-result of the achievement of viviparity has been to enable forms so produced to survive with far more certainty, and to begin their struggle for existence with a greater chance of success than if the complex series of processes of germ-development, in these cases, had to proceed to the same stage without the elaborate means of protection afforded by the parent. This is so obvious that it seems hardly necessary to call attention to the significance of the gradual complication of sexual processes. Yet, as one finds the subject usually dealt with, sexuality seems to be regarded, by the majority of writers, as an ultimate fact, and as such, incapable of interpretation in more general terms.

That sexuality has an important bearing upon some of the most important questions in evolution, no thoughtful biologist would probably doubt. Notwithstanding this, there have been few serious attempts made to grapple with the problem of "sex." Many of the attempts which have been made have failed because of the way in which the fundamental question, sex itself, was ignored. Most of the speculations in relation to sex have been content with determining the effects of self and cross-fertilization, and have accordingly dealt with some of the consequences of already achieved sexuality, but have thrown no light whatever upon the probable origin of sex itself.

Without questioning the high value of the results of such experimental investigations, the question of the origin of sex is probably nearly or quite beyond the pale of experimental inquiry, in virtue of the fact that even the lowest organisms in which sexuality is manifested, are already so persistently adapted to a certain habit of life, and are consequently so fixed in organization that experimental investigation looking to a modification of their reproductive processes through artificial interference is quite impossible within the limits of a single life-time devoted to experimental research. We shall accordingly have to examine the phenomena of sexuality as we find them, and upon careful analysis and comparison try to reach such conclusions as seem to be warranted by the evidence.

Since sexuality leads to processes of discontinuous growth in the production of new beings or offspring, it is of the utmost importance that this very important fact should be kept in mind from the start. That it has a significance there can be no doubt, when considered in connection with the manner in which germs are produced in the various types. The manner in which such discontinuity is effected varies within wide limits and is associated with other preliminary processes, such as the formation of fixed colonies of animal organisms and the multiplication of axes or branches in the vegetable kingdom. One of these two processes is, in fact, usually the prelude to the occurrence of the process of the dehiscence of the definitive sexual elements in a great variety of forms.

When the one process, namely, that of continuous growth of the parent organism, ceases, the reproductive process seems to recur, so that sexual genesis and growth seem to be opposed to each other, as has often been pointed out. The impossibility of otherwise adding or integrating more tissue through the incorporation of more nutriment to a structure already finished, or fully developed, at least for the time being, leads apparently to the recurrence of sexuality. The expression of sexuality is accordingly largely, if not wholly, dependent upon nutrition, and it is from this fundamental standpoint that it will be dealt with here.

It will be equally important to consider the peculiar characteristics of sexual cells. In almost all biological works it is asserted that the germ-cells of multicellular forms are in all respects, at first, morphologically identical with the other undifferentiated cells of the parent body. While this statement is true of the young germ-cells, it is untrue of nearly all mature germ-cells. The latter, in their mature condition, present us with form-elements, either of a size greatly in excess of those of the rest of the body or others which are, invariably within the limits of the animal kingdom at least, smaller than any of the cells of the parent organism. The significance of this fact must also be constantly borne in mind, as well as the equally important one respecting the usual morphological equivalence of myriads of the smaller or male germ-cells and a single large or female germ-cell, in the majority of higher forms.

This frequent, indeed usual, lack of equivalence of the male and female reproductive bodies has been almost entirely ignored by many authors, and has led, as the present writer is convinced, to erroneous interpretations of some of the most important phenomena of subsequent development. The peculiar function of growth of the female cell and its specialized method of segmentation, after the initiation of development, has apparently contained little of significance for the great majority of biologists. Segmentation of the oösperm, as the fertilized egg is termed, is a matter of course with the majority of embryologists, whose work begins with the institution of segmentation and not with any apparent anxiety as to the origin or cause of the thing which segments, and which does little else for a considerable space of time. While the high value of the work done through careful embryological research is to be properly appreciated and is so appreciated by no one more than by the present writer, I believe that embryological teaching and investigation should begin with a consideration of the probable causes which have led to the production of the fully developed and united elements which are usually the subject of the embryologist's study.

The universal occurrence of sexuality amongst all plants and animals, except amongst the very lowest forms, is surely evidence enough, if any were needed, that somehow sex must have been a most important factor in biological development. To say that sexuality was developed solely for the purpose of inducing variability or of favoring fertility and vigor through crossing does not suffice in the face of the evidence presently to be offered. When the defenders of the view, that sexuality was developed in order to favor variability and cross-fertilization, are asked to give any probable reason for the origin of sexuality, the causes alleged are such as have seemed, to the present writer at least, so unsatisfactory that they are hardly worth serious attention.

What, then, was the origin and meaning of sexuality? What were some of the causes which may be reasonably supposed to have been operative in inducing sexual differentiation? Was sexuality differentiated for any purpose, or was its development merely the result of the operation of natural causes? These are some of the questions that the present writer has set before himself to answer, with such light as may be derived from the facts in the present state of our knowledge.

The value of this attempt at an approximation to an answer to these questions must be determined by the judgment of those most competent to form an opinion and the value of the results as a working hypothesis in the hands of such persons.

If, as the writer believes, sexuality has been the means through which morphological complexes or organisms of all sorts, animal and vegetable, have been built up, that alone would be a sufficient reason for a renewed discussion of the subject. If, moreover, the evolution of sexuality, through natural causes, has not only been one of the most important agents in evolution of all the multicellular types past and present, but also the means through which the first possibilities of individual variability, fertility and morphological capability were greatly augmented, it is exceedingly desirable that the evidence upon which such claims are based, should be presented. Finally, if sexuality has led to consequences as far-reaching as these, it is also obvious that its claim to consideration, as a factor in biological evolution, is, perhaps, quite as great as that of the principle of natural selection, to the elucidation and demonstration of which Darwin devoted the best years of his life with a singleness of purpose which has been rarely equaled.

That so strongly expressed a characteristic as sexuality, in both the animal and vegetable kingdoms, should have been developed for mere reproduction, is completely disproved by the data of sexuality themselves. It is clear that sexuality becomes more specialized with the progress of the structural complication of organisms, yet external influences may lead to the suppression of fully developed sexuality. It has been most conclusively proved, that if a species is artificially cared for, in a word, cultivated, as in the case of plants, it may be indefinitely reproduced by means other than those of sexuality. It is even probable that partial or complete sterility has been so induced in not a few plants cultivated for their fruits. The only remaining effect, if effect it can be called, is the impotent fructification of the ovules, whereby the fleshy esculent mesocarp of the ovary or fruit is stimulated to growth and development, for which alone the plant is valued by its cultivator, man. But, so far as I am aware, it has not yet been even proved that such fertilization is necessary.

If parthenogenesis can and does occur in *Cœlobogyne* and in *Saprolegnia*, there is no reason why, even in highly developed monocotyledons, such as the astonishingly productive Banana, in spite of its sterility, should produce indefinitely, through a kind of abortive parthenogenesis and as a result of its great vigor, its succulent but seedless fruits.

If the progressive differentiation or the gradually more intensified expression of sexuality means anything at all, in both plants and animals, beyond providing for mere reproduction, it must mean something of far more utility to species than to provide for variability alone. If the gradual acquirement of viviparity in both animals and plants has any significance, it includes not only a provision for variability, but also achieves the far more important end of providing greatly increased chances for the survival of the thus protected germs or viviparously produced young.

That the young of such forms are more susceptible to the altering influences of outer conditions than the adult is conspicuously established by the evidence drawn from comparatively complex forms. It is well known that the normal alga-like, filiform protonema of *Sphagnum* may, in some cases, become a flat thallus if grown upon a solid, moist substratum. And doubtless, corresponding modifications may be otherwise induced in the further development of its sexual offspring, but of this I know of no direct proof.

That it should have been assumed that sexuality provides for variability is not strange. If one considers the problem of variability from morphological and physiological points of view, the evidence is wholly in favor of the conclusion that increased complexity would favor variability. That sexuality has increased the complication of its attendant processes there cannot be the slightest doubt. If the results have become more complex as viviparously developed germs were evolved, not only would the capacity of those germs to vary be increased in virtue merely of such increased complexity, but the offspring of two parent individuals, differing even very slightly, would also have to be added as a factor favorable to variation.

Unfavorable to some forms of the doctrine of rejuvenescence or that view which regards sexuality as a means of rejuvenating certain cells by means of conjugation or the act of fertilization, are the facts which prove that, in the vegetable world at least, growth may go on indefinitely without the recurrence of sexuality, and with increased, rather than with diminished, vigor. I need only to cite the Banana which has been asexually propagated by cuttings for centuries. The significant and persistent vigor through twenty centuries of a Dracæna, or Dragon's blood tree, is also of interest in this connection. The persistent growth of the asexual generations of tree ferns in the present age and of the gigantic Lepidodendrons and Equisetums of the carboniferous period, shows that conditions of life have much to do in maintaining the vigor of such asexual generations.

Senility, or impairment of vigor, does not then seem to result from continued growth, as is shown by these facts, and this conclusion is equally well established by the facts which are known in relation to the reproduction of the Cyanophyceæ, Schizomycetes and the yeast plant.

This unimpaired vigor seems to be associated with the continuous production of new axes in the higher plants, or with continuous fission of cell-units in the lower ones. In animals, on the other hand, this vigor shows itself most pronounced in the colonial forms (cormi), or in such as are specially nourished, as the Queen Bee or ant-queen of Termites, amongst Anthropods, and amongst which these animals are also the longest lived, and where it finds expression partly, at least, in parthenogenesis. The astonishing vigor of the fertile parents of these forms is largely determined by their abundant nutriment.

The genesis of sexuality, upon final analysis, will probably be found to be a purely physiological question, in the discussion of which the energies represented by the cytoplasm of the egg on the one hand, and its nucleus and that of the spermatozoan on the other, will have to be considered. This will, however, represent only the germinal or embryological side of the problem, which takes no cognizance of the preëmbryonic history of the germinal elements before the latter are set free from the parent. The attempt to formulate the laws of sexuality without examining into the preëmbryonic history of the germinal elements must necessarily end in failure and disappointment. The generative forces at work within the parent organisms are nicely adjusted, or in a state of equilibrium with those which are concerned in the conduct of the ordinary physiological activities of the parent body. It is, therefore, imperatively necessary to consider the question of sex not simply as one involving embryological data, but rather as embracing the sum total of physiological energies of the parent organisms, and where the sexes are separate these energies must be considered as represented in the species by the sexually differentiated individuals composing the latter.

It will be obvious to those who have kept pace with the growth of physical science, that sexuality may be thus brought more nearly within the dominion of purely physical laws. In other words, sexuality is a question involving the discussion of matter and its energy of motion, and should be so treated if it is expected to reach conclusions which are in harmony with the genius of modern science.

That such a project may be accomplished in the present state of our knowledge may well be doubted, yet there is ample reason to warrant making an attempt to clear the ground for further work in that direction.

The attempt to trace the ways in which one form of reproduction gave place to a more complex one in the next higher type is beyond the scope of the present paper. To consider this question adequately would require a far more extensive acquaintance with the facts than is possible at present. In plants it would require a consideration of the modifying effect of the evolution of a mechanical supporting system and the correlative modifications which this must have induced in the sexual processes, since the evolution of powerful supporting axes, which were capable of indefinite growth, dichotomy, and consequent multiplication of fertile apical axes enabled the plant to multiply the possibilities of the production of male and female prothalli, or of protected and attached macrospores and dehiscent microspores. Not only this, but aërial currents would now become available, as the plants become taller, in carrying the microspores, or male prothalli, as pollen grains, from one flower to another. Finally, this was supplemented by flying insects, which, it is fair to assume, first began to visit the plants for the sake of their microspores or pollen as food. Later, as these insects began to set up irritations in the flowers, there is reason to think that the surfaces which they habitually abraded would, if wetted with saccharine solutions regurgitated by such visitants, begin to pour out additional nectar or saccharine matters in obedience to well-known rules of ormotic action. That such a result would happen is, at any rate, strongly indicated by the experimental results obtained by my colleague, Prof. W. P. Wilson, in wetting abraded surfaces of leaves with saccharine solutions. The elaboration of sweets so begun would be a stimulus, causing the insect world to become still more interested in the flowers, and such may have been the further effect of the new diet upon insect life as to be directly responsible for the evolution of those wonderful insect communities developed amongst the honey-loving hymenoptera or bees. The further consequences of entomophilous traits developed by plants must react in other ways, probably through epinasty and hyponasty, in modifying the shapes of flowers, while protandry, a natural consequence of the earlier maturation of the andrœcium, as a lower whorl of the flower, would eventually tend to establish cross-fertilization, through insect agency, as an imperative necessity, and not wholly, perhaps, because cross-fertilization meant the production of a more vigorous offspring.

The gradual evolution of sexuality by slow stages in plants is now so well understood, that it is not necessary to enter into the details which may be found in any standard botanical text-book. It is sufficient to indicate that the transition from asexuality to female macrogonidia and male microgonidia is effected by mere differentiation of cells as respects their size. From naked oöspores to carpospores is the next step, with microscopic flagellate male elements. Finally, the prothallus appears, first, with both oöspheres and antherozoids ; then the prothalli themselves become distinguished as small male and large female ones ; then the female prothallus is no longer at once detached, but becomes covered in, while the minute male prothallus still dehisces, but finally becomes partially parasitic upon the stigma where it vegetates and throws out a hollow process, which serves to convey the now highly modified antherozoid to the ovicell. The prolonged adherence of the female prothallus to the parent axis enables the next important step to be taken in the evolution of the seed containing a viviparously produced embryo provided with a store of nutriment and protective envelopes.

In this way the superimposition of more and more successful means of reproduction seems to have occurred in plants, tending also to secure the final victory of the phanerogams over all other rivals in the struggle for existence, largely through the evolution of viviparity as supposed above. How much of this success was due to the principle of overgrowth or cumulative integration, which made rapid, continuous assimilation and growth possible through the evolution of a mechanical supporting system, is hard to tell, but it doubtless was quite as important a factor as natural selection itself.

Similar conclusions are borne in upon the zoölogist in a study of the reproductive processes in the animal world. From asexual fragmentation and consequent multiplication, the advance to larger and smaller, or female and male elements, was a gradual one, with or without hermaphroditism. Then came hermaphroditism with large female and small male germs, then maleness and femaleness, as characterizing distinct individuals of the same species. Finally, protective processes were developed, accompanied by ovulation, followed by parental care, such as incubation, nidification, gestation with or without placentation, and at last, in the highest forms, lactation was developed.

These processes seem to have grown up as if superimposed upon each other, just as it can be shown that the progress of embryological ontogenetic development has followed as a consequence of the superimposition of one morphological complication upon the immediately preceding one, and often as a consequence of direct adaptation. Similarly, the inclusion of the germ tracts, as morphological advances shut off the gut-pouches from the archenteron, became more decided. The complexity of the outlets for the reproductive products, at first by way of the nephridia, as these were fused into a serially connected system, became more marked, the sexual products were now discharged through the passages serving also for the emission of the urinary secretion. Finally, this passage became divided lengthwise, so as to serve for the separate discharge of the urinary and sexual products, until at last the lower end of the reproductive channel became modified into a brood chamber or uterus for the viviparous development of the young, accompanied with sexual intercourse, now rendered possible by the further modification of the extreme outer portions of the reproductive passages and the parts immediately adjacent to them.

Pari passu with the higher development of the reproductive processes the fertility of the female became absolutely reduced, partly in consequence of the precocious overgrowth of the female germs through a primary suppression of the tendency to spontaneous segmentation of such germs, as will be more fully illustrated later. This reduction in the fertility of the female gonads is also doubtless correlated with the increased chances of the survival of the offspring produced by the more protective methods of reproduction, while the material diverted from ovogenesis, to carry on the formation of secondary egg-envelopes, incubation, nidification, gestation, placentation, lactation and other parental care, also reacts directly upon fertility, while the great lengthening of the period of fœtal and infantile development, tends to still further reduce the possibilities of rapid reproduction. The recurrence of the seasons tends to make the reproductive periods annual in all forms except the lowest asexual, and the highest form, man, who lives under approximately uniform artificial conditions of his own creating. There is, therefore, a widespread tendency toward a reduction of the fertility of most forms below what it would be if there existed uniformly favorable conditions throughout the year, due solely to the recurrence of unfavorable annual periods.

The fertility of the male, or rather his functional activity, may be affected in a corresponding manner by the seasons, but the absolute fertility of the male as compared to the number of germs produced is invariably greater than that of the female, usually by many thousandfold. This greater male fertility depends upon the minute size and rapid production of male elements through the breaking down of protova—spermatogonia—and the rapid integration of chromatin or nucleoplasm as will be shown later. Such a rapid and abundant production of male elements may be one of the causes leading to the persistent pursuit of the female by the male, and one of the causes of the genesis of sexual passion as interpreted farther on. Sexual passion, which accompanies the highest forms of reproduction, finally becomes functional in this intricate series of superimposed processes as a means tending to maintain the fertility of all the females of a species at its highest point of efficiency, and thus reacts as an aid in the survival of species. The superabundant fertility of the male renders the possibility of the conjugation of the male and female elements more certain, under the favor of the various devices which have been evolved to effect that process, and thus again be the means of assuring reproduction and the survival of the species.

The necessary correlation of the male and female is probably secondary. In my view, that the flagellate forms are the oldest, since they are certainly the simplest and minutest, the male element represents, morphologically, a perpetuation of the most primitive form of organized existence. Through cumulative integration the germ elements, which would otherwise have tended to break down into flagellate germs, have, on the contrary, been impelled to grow to large dimensions as ova, through the rapid access of nutriment to them, which probably prevented their cytoplasm from having time to elaborate nucleoplasm and chromatin, and thus become male in character. The male element is certainly the most ancient, the female is a secondary and later product of evolution. The correlation of the male and female was, therefore, secondary; the male elements represent, morphologically, the primordial asexual type. The primitive representative of the male element was at one time "maternal," through simple fission and a capacity for growth; it became "paternal" through conjugation. Sexuality was the outcome of the unequal growth of germ-cells of the same species, induced by the self-regulative influences exerted by internal physiological conditions operating under the influence of varying external conditions. The determination of the sex of an embyro has depended in some way upon a tendency, early established through some internal equilibration of the forces of growth, in response to outer conditions of nutrition, etc. There is no conclusive evidence tending to show that the sex of an embryo is predetermined in the egg; on the contrary, much evidence exists tending to show that the sex of an embryo may be influenced by an increase or diminution of the supply of food.

It is a curious circumstance to note that many writers on sex seem to have failed to see that the sexual cells of multicellular forms were functionless, in that they exercise no physiological function which is essential to the life of the parent organism. In that such functionless cells could not disintegrate their substance through the active metabolism which obtained in respect to all the other cells of the body, in consequence of the action of the principle of cumulative integration or assimilation beyond the current physiological needs of the body, they must either increase enormously in size and become ova, or run down as a result of rapid karyokinesis into minute male elements which are rapidly dehisced and set free. It is this exemption of the germ-cells from the disintegrating effects of active or functional metabolism which has given the first impulse to the accumulation of yolk and the overgrowth of the spermatogonia, ending in the production of the ovum and the essentially female condition. The apical position in many plants of the female germ is significant in this connection, no less than the fact observed by Mr. Meehan, that in conifers the female flowers are produced at the apex of the tree and by the most vigorous shoots.

The Origin of Karyokinesis, the Significance of the Polar Bodies, Variability, Sexual Passion and Sex in Relation to the Genesis of Species.

It is a remarkable fact that in the lowest forms of life no evidence of karyokinetic changes has ever been noticed. Spores are produced within the body of the parent individual by the direct fragmentation of the slightly more chromatophilous or deeply staining portion of the parent plasma that fills nearly the whole of the latter, so that it is still not possible to speak of a nucleus in contradistinction to a cell-body of cytoplasm in these organisms. These facts tend to show that in such very low forms there is still a want of mobility of the plasma itself as well as a lack of differentiation into nuclear and cytoplasmic matter.* Is or is not the want of a differentiation of cytoplasm associated with the absence of karyokinetic phenomena? There is much reason to assume that it is from the consideration of a great variety of facts, mainly those observed in the earlier stages of development of higher sexually produced forms.

The main argument in favor of such a view is the circumstance which has fallen under the eyes of every investigator, that the karyokinetic phenomena are most pronounced in the earlier stages and on a larger scale than in the later stages when the cells become smaller. This is either associated with a larger proportional amount of cytoplasm or it is independent of it. So far as observation has extended, the facts of early segmentation tend to favor the first alternative of the foregoing proposition. Another body of facts is equally favorable to such an interpretation, namely, that of spermatogenesis. It is true that many forms of spermatogenesis are known where karyokinesis is maintained up to the time that the spermatic elements are beginning to form, but there are many other cases known where this is not the case and where during the later stages of spermatogenesis leading to the fragmentation of the spermatogonia there is no evidence of accompanying karyokinesis. These facts tend to show that, with the gradual diminution of the amount of investing cyto-

* De Bary, in his Lectures on Bacteria, affirms that a nucleus is wanting in the Schizomycetes, and the only case where these forms have been known to exhibit amœboid movements, so as to throw out processes, is that described by Prof. Samuel G. Dickson, of this city; at least I have been unable to find any other instances of the kind described. There appears to be little cytoplasm in these forms, so that these organisms correspond mainly to the nuclei of the cells of higher types.

plasm, the process of karyokinesis or movement of the fragments of chromatin is finally restricted to such an extent, from the want of a cytoplasmic field, that nuclear movement is at last rendered impossible.

Much as the lengthening of the spermatozoön resembles a diastolic phase of karyokinesis, there is no evidence that the elongation of the male element preparatory to being set free, can be identified in any case with such a final karyokinetic diastolic phase. If this were so it might be supposed that the momentum of karyokinesis, in this case, had reached a potential state or condition of tension ready to exhibit itself as segmentation, as soon as there was a large enough cytoplasmic field, as in the cytoplasm of the egg, in which the opposite condition of systole could occur, and thus bring back the nucleus to a condition of equilibrium.

While the foregoing conclusion cannot be assumed, it may be assumed that the male cells, in undergoing their rapid multiplication, do acquire a certain karyokinetic momentum predisposing them to set up segmentation in other functionless plasmic bodies—ova—which they may enter. Yet, as we have seen, karyokinesis is not always an accompaniment of spermatogenesis, a condition which may arise, as supposed above, from the gradual diminution of the cytoplasmic field.

The method of evolution of spermatozoa is not uniform in all cases. In *Ostrea edulis* there are rarely individuals in which spermatogenesis approximates that of *O. virginica.* Then, rarely, intermediate forms occur between this and the normal form, where large masses of chromatin are formed by direct elaboration from the nuclei of elements which cannot be regarded as other than ova. In the latter case the metabolism which leads to the development of spermatozoa is clearly carried a step further than in ovogenesis, because the huge masses of chromatin imbedded in the ova from which the nuclei of the spermatozoa are formed are very certainly developed *after* the stage is reached which answers to that of the mature ovum. The male condition is reached therefore in this last case after the female, and is an outgrowth of the latter consequent upon the development of large masses of chromatin in the egg and its direct fragmentation into the nuclei of spermatozoa. In those cases where the spermatozoa are developed more directly from smaller cells which never reach the dimensions of ova, we have a totally different case, and one which indicates a protandrous tendency. The other case where the male condition depends upon the previous development of a fully differentiated female state of the germ-cells obviously corresponds to a protogynous condition.

The formation of chromatin in the last case does not proceed as a result of metabolism and growth following a rapid series of karyokineses alternating with periods of rest, but follows the formation of a female nucleus in which a rapid endogenous formation of chromatin first occurs, followed, as it increases in bulk, by the extrusion of the chromatin from the parent nucleus into the surrounding cytoplasm, where it breaks up into small masses which are later separated in large groups as the nuclear basis of large coherent clumps of spermatozoa.

Clearly, then, the amount of chromatin in relation to the amount of cytoplasm varies all the way from an almost inappreciable quantity in the nucleus of the true egg to a very great quantity in proportion to the cytoplasm in the egg which produces a large quantity of chromatin from its nucleus to provide the material for the nuclei of the multitudes of spermatozoa to which such an egg gives rise.

Maleness, therefore, in the case of *Ostrea edulis* is certainly, and probably in all other forms, a condition where the chromatin preponderates over the amount of cytoplasm, while, conversely, femaleness is characterized by the preponderance of cytoplasm over chromatin or nuclear matter ; that is to say in the sexual elements only.

Such a preponderance is not simply relative, it is absolute as respects the one or the other of the primary germ-constituents. It is also a fact that the amount of chromatin or nucleoplasm in an egg-nucleus, when nearly mature, is in excess, as expressed in volumes, by at least four times that of the chromatin contained in the mature male element of the same species. Does this last fact signify anything in reference to the expulsion of the polar bodies? It probably does if the interpretation of the polar bodies presently to be offered is true. And that that interpretation probably is true or more nearly true than any other yet offered, will become clearer as we proceed, since it imports nothing into the discussion of the data which is not in conformity with the facts of continuous growth or which must be brought in in order to save previously suggested hypothesis. It postulates only continuous growth under the condition of an excess of nutrition beyond that required in the secular exhibition of the physiological activities of living forms. It supposes that this excess is somehow influenced in one of two ways, that is, it is either preponderatingly converted into chromatin or preponderatingly into cytoplasm.

If mainly into cytoplasm, the process may go on until the cytoplasm itself may tend to run down chemically into the more stable conditions of oils, or yolk granules and tablets consisting of simpler molecular units. This last process may go on until an enormous yolk is developed which is composed of inert or immobile nutritive matters, while the active cytoplasm itself may become small in amount and reduced to a relatively small volume.* Such a process never occurs in the male. Here karyokinetic processes keep the upper hand (not necessarily katabolic ones, or those leading to destructive metabolism), and the result is that the male element tends to be reduced in dimensions with no katabolically simplified contents, such as are met with in many eggs, but, on the contrary, consisting mainly of plasma in a highly anabolic condition as chromatin.

How these differences on the sexual elements are produced is not known, but it is certain that they must be produced by the action of the physio-

* This is so clearly in its general features a katabolic process, that it is impossible to see how Geddes and Thomson can reconcile this with their hypothesis that the egg is anabolic, while the male element is essentially katabolic (see their work, "The Evolution of Sex," New York, 1890.)

logical activities of the parent organism modified or swayed toward maleness or femaleness, through some series of correlated influences which are self-regulated in some way through nutrition, in the struggle of the parts of the parent organism with each other for their allotment of nutriment.

So far, the evidence tends to indicate that the egg is a repressed condition of maleness. That is, the high anabolic condition of the male element is the consequence of unimpeded growth resulting in rapid segmentation, while the female element is in some respects katabolic with an unimpeded growth of its cytoplasmic constituents accompanied by a repression of the capacity for segmentation.

The peculiar conditions of growth of the egg, and its usual trait of great size, constitute probably the real essence of the meaning of sex, as a means of favoring, in an increased ratio, the survival of offspring.

The preponderance in the actual volume of the chromatin of the egg, over that of the spermatozoön, expresses a physiological differentiation not reached by the latter so much more quickly matured. This might be due to the fact that the cytoplasm in the male element is smaller in amount than that of the egg, and may be coördinated or physiologically controlled by less chromatiu. On such a basis the hypothesis of Minot and Balfour might be rehabilitated in part, but not on the erroneous basis of sexuality as they supposed, but upon the far more significant one of physiological differentiation or division of labor.

Maleness is characterized, in the male element, by the absence of a cytoplasmic field in which nuclear motion or karyokinesis can occur. With this in the male element goes an inability, after sexuality is fully established, to maintain further nutrition and growth without the help of the female element.

Femaleness, on the other hand, is characterized by the presence of an enormous cytoplasmic field in the midst of which there is placed a large nuclear body containing proportionally to its envelope of cytoplasm a very small amount of chromatin. Such a germ is incapable, except under the antecedent stimulus of exceedingly vigorous processes of growth, as in the case of parthenogenesis, of spontaneously beginning and maintaining an orderly process of karyokinetic movement leading to further metabolism growth and development, unless "fertilized" or fused with the male element.

The tendency in the male cell is towards a preponderance of chromatin, in the female cell towards a preponderance of cytoplasm. The elaboration of the chromatin in the male clearly takes place in some cases at the expense of cytoplasm ; the elaboration of cytoplasm in the female is possibly at the expense of chromatin, and certainly at the expense of the prolonged exercise of the function of the latter as an essential part of the egg nucleus.

These processes in the two sexes admit of further contrasts. The cytoplasm is mobile and amœboid and the immediate instrument of intussusception of new material. The chromatin, on the other hand, while appearing to centrally control this process, is never immediately, but only mediately involved in its execution. No cases are recorded where the chromatin shares directly or immediately in the process of digestion or intussusception of new matter, except possibly the Bacteria or Schizomycetes.

The female cell previous to final maturity has been involved in the accumulation of the cytoplasm; in this process its chromatin has been indirectly involved and has increased in volume proportionally. This same fact is illustrated in the increased dimensions and complexity of the nucleus as growth in cytoplasmic dimensions increases in even such simple forms as *Amœba*, as may be clearly seen in Leidy's monograph upon the Rhizopods of North America, where the changes in the relative proportions and arrangement of these substances are fully illustrated in the progress from the young to the adolescent stages.

There is therefore ground for the belief that there is a certain minimal proportion of chromatin necessary for every cell which is necessary to maintain its physiological integrity. In the egg cell the chromatin must share in the constructive metabolism involved in the prolonged growth necessary to mature the ovum. It is not improbable that this function of sharing in constructive metabolism and not in that of karyokinesis has rendered the egg incapable of spontaneous segmentation, unless it be the product of a tremendous energy of growth and conditions of assimilation, as in the case of parthenogenetic ova.

Not only the chromatin, but also the whole of the rest of the nucleoplasm of the egg, is probably, like that of any other physiological differentiated cell of the parent body thus rendered in most cases incapable of undergoing immediately the spontaneous changes necessary to cause the beginning of development.

The equilibration of forces leading to the growth of male and female elements, respectively, in the parent organism is in some way self-adjusted or self-regulated. It is probably true that in many cases there is good reason to assume that the eggs are more favorably situated in reference to supplies of nutriment than the spermatogonia, or conditions subsist which tend to repress spermatogonial segmentation.

Such a view may be fortified with a great host of facts drawn from the relations of the male and female reproductive organs, in many forms, to the sources of nutriment. In many cases the ovaries are clearly in a more direct and favorable relation to the sources of supply of nutriment than the testes, as in many Bryozoa, for example. Or the source of supply of nutriment for the reproductive organs is more remote for the testes than it is for the ovaries, as is actually the case in many forms, notably a large proportion of mammals where a *descensus testiculorum* supervenes. Or, in other cases, the surplus nutritive matters are competed for within the organism by structures which are usually described as belonging to the category of the secondary sexual characters. Or, in another very large class of data, we have evidence tending to show that the ovum is placed under conditions of growth, or is encapsuled within a porous basement membrane—the zona radiata—so as to favor from every point on its surface its cumulative growth in bulk, rather than its cleavage or segmentation within the parent, which would end in its breaking up into male elements. The male elements, on the other hand, are not encapsuled, at least in a very large proportion of cases, and are free to grow in another way without an intracapsular repression of karyokinetic processes. It would be an easy matter to cite multitudes of facts in support of the argument here offered, though I am aware that strong counter-arguments might be produced, yet I do not believe that they are anything like as weighty as the affirmative evidence.

Again, all the facts tend to prove that the recurrence of male forms in parthenogenetic types is associated with a decrease of the supply of nutriment and a slight lowering of temperature.

How do these facts comport with the data in our possession respecting the manner of development of the characteristic male plasma or chromatin? We find that after a certain limit of size has been attained by the egg or spermatogonium in *Ostrea edulis* that the evolution of chromatin begins and with this process the production and freeing of spermatozoa. It looks as if the chromatin or characteristically male plasma required a longer time for its elaboration than the cytoplasm, which is in consonance with fact. In other words chromatin can be formed only from previously elaborated cytoplasm, and the latter when its sources of nutriment are cut off or diminished tends, in virtue of its freedom from any functional duty in the parent body to be built up into a still more complex molecular form, as chromatin. Or the struggle of cells in the gonads for nutriment may tend towards the male condition provided all take part, and spermatozoa result; if only a few take part in the struggle, under encapsuled or other conditions unfavorable to the elaboration of chromatin and karyokinesis, the female or large celled type of germ is formed.

That something of this nature must occur is evident if we contemplate the problem from the purely morphological side, but with the physiological aspect of the matter still in view. The chromatin is primitively the most central element of the plasmic contents of the cell. It is the most homogeneous of all cell contents; it is least like an emulsion of any of the cellular constituents. In that it is the most distantly removed from the periphery of all the cell-contents and the latest to appear when developed in great quantity from the nuclei of egg-like spermatogonia, it is the highest and latest product of cellular metabolism. It is therefore clear that the element of time is to be considered, and that chromatin or the most characteristic plasmic basis of the male element is the end-product of the untrammeled exhibition of the energies of functionless or sexual protoplasm. It is upon this ground that it is safe to assume that the male element is the primary one and that the female element is secondary and has arisen through a repression of the processes which lead to the metamorphosis of cytoplasm into chromatin. The male state is therefore the oldest; the female the youngest. The male state also as represented in the spermatic body tends to revert to the most ancient form of all free mobile organisms, namely, the flagellate Schizomycetes. The tendency towards maleness is therefore also to be identified with a universal tendency of all organisms to recapitulate the most ancient and primitive of living conditions when organisms existed only in watery or fluid media. The further generalizations that all organisms tend to recapitulate the primæval monadiform condition is also fully justified, and that the really primordial type of the germs of all living forms is a flagellate cell and not an ovum. This will become clearer, as it will be later shown that the ovum is secondary and is really a germ which has been arrested in its attempt to reach the flagellate condition, and that the polar bodies are merely the expression of an expiring tendency in the egg to revert to the male or primæval flagellate condition.

The genesis of sexuality itself is merely incidental to the continuous processes of growth manifested by all living forms. It is an outgrowth of self-regulated processes of nutrition and of the repulsion of accumulations of surplus nutriment to parts of the organization of multicellular forms where it is not in the way of the other physiological activities. This is the real significance and origin of the process of the isolation of germinal matter. It is not a "device" or an "expedient" specially contrived for the preservation of the immortality of "germ-plasma," which was not first "set aside" in Metazoa, as held by Weismann, but which began to be pushed aside and out of the way in Protozoa, as many facts show even as low down in the scale as Amœba, thus placing Lendl's criticisms of Weismann upon the basis of fact.*

We have seen that the female and male germs can be actually contrasted only on the ground that they are constituted of two kinds of plasma in different proportions. We have also seen that the chromatin presumably preponderates in the lowest living forms, which are also universally asexual but capable of the most prodigious rates of multiplication owing to rapid growth of their substance (mainly chromatin-like) under favorable conditions. These lowest forms are also flagellate, probably universally so under certain conditions. In the next stage of evolution the tendency is for certain cells to grow to a large size and then break down into flagellate spores which are alike and constitute the germs of the species. The next stage is where certain of these enlarged cells break down into flagellate spores of unequal size, the larger become female and the smaller male and incipient sexuality is developed. The process may even begin with the conjugation of similar binucleated individual cells, as in ciliate Protozoa, but there again the production of the spermatic plasma

* In this connection see Brass, "Die Zelle das Element der Organischen Welt," pp. 63–65. Leipzig, 1889. Also Lendl, "Hypothese über die Entstehung von Soma- und Propagations-Zellen." Berlin, 1889. Also Lillie E. Holman, "Observation on Multiplication in Amœbæ." Proc. Acad. Nat. Sci. Philad., pp. 346–348, 1886. Leidy's "Rhizopods N. America," where the chromatin balls of the nuclei are figured as being expelled from the nucleus and the animal presumably as germs.

or chromatin proceeds in a way which may be compared to an endogenous or intraplasmic fragmentation of the chromatin substance, part of which is probably not functional as the nucleus, so that even here the germinal matter is "set aside" contrary to the assumption of Weismann, who only finds such a process taking place in Metazoa. These binucleated forms have one macronucleus functional and another sexual micronucleus which is not functional in the ordinary life processes of the species. It is this latter which multiplies and grows at the expense of the cytoplasm of the parent cell, so as to form not only the material for the new micronucleus but also that of the new macronucleus, the old macronucleus when exhausted being disintegrated and absorbed by the cytoplasm. In this case the process of conjugation signified a reconstitution of the exhausted macronucleus, a process which always occurs in some forms only when the cytoplasm of the parent is free from unelaborated and non-assimilated constituents. An excess of chromatin and nucleoplasm is produced, part of which becomes the functional nucleus and part is thrust aside as a quiescent functionless body, the micronucleus. When conjugation occurs it acts as a stimulus, causing the rapid growth and division of the micronucleus at the expense of the cytoplasm of both individuals which are not feeding during this process. The reconstitution of the nucleus is therefore to be interpreted in terms of continuous growth and as a physiological process which is directly adaptive under the conditions of morphological differentiation attained by these organisms. The reciprocal fusion of one of the nuclear bodies produced by a subdivision of the micronucleus is to be understood in the way which will be indicated later.

The death and loss of the power of coördination of movement shown by the cytoplasm of lower unicellular forms, when the nucleus with its chromatin is removed, simply demonstrates the transcendent physiological importance of the nucleus as a directive centre. This view is also sustained by the fact that ultimate nerve terminations in the Metazoa are lost in some cases within the nucleus. The effects produced by the artificial removal of the nucleus in impairing the power of growth and reproduction are due to the destruction of the physiological equilibrium between the chromatin and cytoplasm as well as the morphological integrity of the individual. It does not necessarily mean that the nucleus is the reproductive agent, but rather that this highest end-product of protoplasmic metabolism is the central object for which the investing cytoplasm labors. Neither can, probably, become the centre of reproductive energy or the energy of growth in absolute independence of the other, notwithstanding the fact that there is an apparent absence of the nucleus in Monera, while the cytoplasm is reduced to a minimum in Schizomycetes.

The conjugation of ciliated Infusoria therefore becomes plainly a process wherein the nucleus has the usual reproductive function through division of labor coupled with an adaptive arrangement by which a physiological substitution of an old for a new nucleus is effected, while the act of conjugation is merely the stimulus through which the active functions are diverted into another channel ending in the metabolism of both individuals manifesting itself in the production of a larger amount of fresh chromatin, capable of taking upon itself the work of the former nucleus, a part being pushed or "set aside" as a functionless surplus ready to be stimulated to growth through conjugation. Maupas' theory of senescence may therefore be regarded as in the highest degree probable, in that in those cases where conjugation has long been in abeyance the stimulus of growth leading to the production of an abundance of chromatin has been absent. From this point of view the Infusoria present a most specialized type of reproductive activity in which the cytoplasm and chromatin have never been freed or separated from each other as marking independent sexual states in which these two cellular constituents have preponderated, as the female and male respectively. In other words, the Infusoria are practically oösperms which are reciprocally stimulated to reproductive activity through the act of conjugation.

The ovum of the Metazoa is in the same case with the Infusoria, but behaves differently because it is purely an ovum. Here the polar bodies are to be regarded as exhausted chromatin or nucleoplasm with a decidedly male tendency in that the cytoplasm investing them is usually small in amount. The polar bodies are to be regarded as representing not only the disintegrated macronucleus but also the disintegrated fragments of the first or preparatory stages of division of the micronucleus. While the products of the fusion of the pronuclei of Infusoria again contrast with the fusion products of the pronuclei of Metazoa, in that they are at once divided into a functional or physiological and a functionless or reproductive nucleus. In the Metazoa the separation of reproductive functions from the other physiological ones is effected through cell-division and does not coëxist in two nuclei lying side by side in the cytoplasm of the same cell.

Nevertheless, there is reason to believe that the chromatin of the egg is partly exhausted, as it is in the Infusoria, and must be got rid of in part in order to regenerate the remaining chromatin through a process of growth accompanied by active karyokineses. This exhaustion supervenes upon the prolonged exercise of its physiological function in building up a large amount of investing cytoplasm under conditions which have interfered with the normal segmentation of the whole into cells no larger than those of the rest of the body. The characteristic overgrowth of the ovum beyond the size of its companions in the body of a Metazoan, is the real ground of the specialization of the egg through which it may be supposed that part of its nuclear matter has been exhausted through prolonged exercise of the physiological functions of the nucleus. It will be seen that this view is similar to that of Weismann, but it is more specific. Accordingly the degree of specialization of an ovum must influence the extent to which its nucleus is exhausted. Parthenogenetic ova are for obvious reasons to be regarded as less specialized than those which are not parthenogenetic. This hypothesis therefore fits in well with the fact of the decrease of the number of polar bodies in the eggs of many parthenogenetic forms, in which the period of growth of the eggs is often shortened, and where the physiological function of the chromatin in the constructive metabolism of the egg is exerted over a less prolonged period. The result is that the exhausted chromatin or nucleoplasm which is to be expelled from some parthenogenetic ova is just half that of the other type requiring fertilization. Such a separation and regeneration leave enough chromatin or nucleoplasm behind to initiate development by beginning a spontaneous and continuous fission of the egg without the access of the male element. This I believe, however, to be only a partial explanation of the causes leading to the expulsion of the polar bodies, since the genesis of the ovum itself remains unexplained. The specialization of the ovum and its hypertrophy as a cell is connected in another way with the operation of the processes of continuous growth, and with the evolution of the primæval form of germs which were unquestionably flagellate. That the ovum is the most specialized cell of the two kinds of sexual cellular types found in Metazoa there can be no doubt.

If it is true that the only thing that stands in the way of the development of any cell of the body into a germ is its physiological and morphological specialization, then the egg with its mass of cytoplasm in excess of that of any cell in the body is certainly a morphologically and physiologically specialized cell-unit. The expulsion of the polar bodies brings it back to an unspecialized condition, in which its nucleus (the female pronucleus) no longer bears any imprint of its former physiological specialization which it had acquired during the elaboration of its bulky mass of cytoplasm.

The history of the spermatic body, or cell, is exactly the reverse of the preceding. If protandrously developed, karyokinetic or fissive processes go on more rapidly from the start than processes of growth through constructive metabolism and spermatozoa result. If the spermatic body is produced through a protogynous process and from large cells simulating ova, the fissive tendency again finally obtains the upper hand, but only after a certain maximum size of the female cells is reached, when they may be recognized as ova. The tendency towards maleness is thus constantly against any persistence of a condition favoring constructive metabolism in the direction of the elaboration of cytoplasm. In fact, so rapidly does the fissive process go on, that the nuclei of the spermatic or male cells have no opportunity to acquire any physiological function, such as that enjoyed by the nucleus of the egg. The tendency in the male cells is rather to intensify the tendencies of metabolism towards the elaboration of chromatin only, carrying the latter process so far that little or no field of cytoplasm finally remains in which fission or nuclear movement can occur; nay, many instances are known where even the remaining remnant of the cytoplasm is cast off from the spermatozoön previous to maturity, this being in exact contrast again with the extrusion of a part of the egg's chromatin as polar bodies. The rapidity of the successive processes of fission in the course of the development of the male cell is such as to give its quiescent nucleus, in its restricted cytoplasmic field, a karyokinetic momentum, so to speak, which will be expressed as segmentation as soon as it is fused with the female pronucleus in a large cytoplasmic field, in the egg, where karyokinesis or nuclear motion again becomes possible.

In the same way the tendency towards developing a karyokinetic momentum must occur in the egg, owing to the limited number of rapidly successive karyokineses in the expulsion of the physiologically differentiated chromatin in the form of the polar bodies, which may themselves manifest subsequent spontaneous segmentation, or even make abortive unions with spermatozoa, which are abortive only, probably, because of the small size of the cytoplasmic field. If the results of Hertwig and Boveri in fertilizing non-nucleated fragments of the cytoplasm of the eggs of Echinoderms are correctly reported, it is certain that the spermatozoön is in a condition of karyokinetic tension, which lacks only a cytoplasmic field in which to find expression as segmentation.

The views here developed also harmonize with what is known of the behavior of the nuclei of conjugating *Infusoria.* It is only the *micronuclei* or *paranuclei* which enter into the reciprocal conjugation. The macronuclei or functional centres of control of the physiological energies of these animals never enter into the process, but are disintegrated and lost in the cytoplasm, while some of the new micronuclei now formed become, after conjugation and reciprocal fertilization, the new functional or physiological nucleus, and one or two remain, for the time being, at least, as passive, and probably functionless, micronuclei.*

It may be supposed by some that the foregoing account is merely a recapitulation of Weismann's hypothesis respecting the significance of the polar bodies. Not so; Weismann's very elaborate and artificial methods have no charm for me. He is continually trammeled by his own cumbersome hypothesis of a germ-plasma. But he is probably right as far as assuming that the first polar body represents chromatin of a "histogenetic" character, but I should say in a totally different sense from that which he implies. I should also agree with him that it is expelled in order that the egg may revert to its unspecialized condition, but again in a widely different sense from that which he holds.

Unfortunately for Weismann, he renders his hypothesis utterly improbable from the necessity of working out a second hypothesis to account for the expulsion of the second polar body, in order to save his first unfounded assumption respecting the immortality of the germ-plasma. That doctrine, driven to its logical conclusion, leads ultimately to the molecular disintegration of the vast series of ancestral plasmas, finally present in the egg in the course of a vast series of generations. Accordingly the only way to save his hypothesis was, as soon as certain parthenogenetic

*In this I follow the recent researches of Maupas: "La Rajeunissement Karyogamique chez les Ciliés." Arch. Zool. Exper. et Generale. 2e Ser., Tome vii, Nos. 1 and 2, 1889. Pp. 149–320 *et seq.*

eggs were discovered by him, to expel only one polar body; to make use of this new fact in such a way as to make the expulsion of the second polar body in perfectly sexual forms, remove a certain proportion of the ancestral germ-plasma, else, in time, the subdivisions of the ancestral plasmas would ultimately be so great in number as to destroy, by repeated division, the molecular integrity of the molecules representing such ancestral plasmas. Unfortunately for such an hypothesis, Nature does not work through foresight and does not anticipate such difficulties, and he is unable to produce the slightest evidence that she does. Organisms do not possess the power to foresee the remote consequences of their processes; they respond directly to conditions, or not at all.

The logic of this argument of Weismann is exactly similar to that used by Balfour in reference to the polar bodies in his "Comparative Embryology" (i, p. 63), when he says "that the function of forming the polar cells has been acquired by the ovum for the express purpose of preventing parthenogenesis." This implies that the egg possesses foresight of harm coming to it through falling into a parthenogenetic habit! And when Weismann proceeds to elaborate his necessary hypothesis of a reduction of ancestral germ-plasmas, and says "this *must* be so," he seems to forget altogether about the probably self-regulating physiological factors controlling the dimensions of cells and their proportions of chromatin and cytoplasm.

The same difficulty was perceived in a somewhat different form and very pointedly alluded to as fatal to the hypothesis of pangenesis, as early as 1878, by Prof. J. Clerk-Maxwell, in his article, "Atom," in the third volume of the "Encyclopædia Britannica," p. 42.

Lately, however, Platner's discovery that in *Liparis dispar* parthenogenesis occurs with the extrusion of *two* polar globules, is sufficient to render Weismann's hypothesis as to the significance of the second polar body thoroughly untenable.

There is clearly nothing left but to suppose that the polar bodies are an expedient through which the egg returns to a condition of equilibrium different from what it possessed prior to their expulsion. We have no warrant whatever for assuming that this return is other than automatic or comes from other than self-regulated impulses arising within the ovum. Such impulses are very probably merely a manifestation of the attempt to recur to and maintain a continuous process of growth, in the course of which the production of polar bodies is only an incident.

The physiological impulse from within which effects this equilibration works, if my hypothesis has any value, as if certain parts of the egg were to be excreted. In fact, if the hypothesis that the huge mass of cytoplasm represented by an egg is a highly differentiated cell-product, resulting from a very prolonged activity extending sometimes over many months, or even years, of the nucleus and its chromatin, while the spermatic body is produced in a much shorter period, it must necessarily follow that the controlling central nuclear body of the egg would undergo a corresponding greater specialization and differentiation than that of the spermatozoön.

This view then satisfactorily accounts for the expulsion of the polar bodies and also gives some indication of the significance of the reduction of the cytoplasm of the spermatozoön or its complete loss, if we regard the egg and spermatozoön as antipodal expressions of a physiological process of evolution, which has resulted in forming bodies which are complementary to each other in every physiological trait which they present.

Since spermatozoa, also, are very often produced from what are manifestly ova, by the breaking down of the latter and the augmentation of their chromatin, it is clear that the spermatic body is a product derived from the egg by carrying its cleavage farther either by means of the direct or indirect method, but while still attached to the parent or nourished by it. From this consideration it follows that the egg and spermatic body are not homologues before the final maturation of the former. It is, therefore, useless to expect to find any structures thrown off by spermatozoa which are complementary, in the sense implied by Minot and others, to the polar bodies of the egg.

As I have been led to the views expressed above by following a totally different path from Weismann, and as I reject his hypothesis of the physiological isolation of the germ-plasm on the basis of fact, as shown elsewhere,* as incapable alike of proof or of serving a better purpose than a much simpler hypothesis, it seemed best to continue the argument upon the lines begun in earlier papers.

It may, however, be well to point out here that what Weismann means by his "histogenetic" or "ovogenetic" nucleoplasm, I distinctly limit to the genesis of the huge cytoplasmic field or cytoplasm and yolk of the ovum. The egg membranes are basement membranes and it is difficult to say what share the egg had in their formation except in lower forms, so that they are of far less consequence in this discussion than Weismann supposes.

Another point is that parthenogenetic ova are certainly smaller than the fertilized ova of the same species, in some forms, though this is not always the case. This fact, however, is in accord with the hypothesis of the polar bodies set forth above. The mode of feeding the queen bee † shows, also, that parthenogenetic eggs, or those capable of developing in that way, are probably produced through the expenditure of less energy in the parent organism than those which develop only in the sexual way in strictly sexual forms. The connection of these facts with the explanation offered of the expulsion of the polar bodies is so obvious that it hardly needs to be indicated.

It has been made clear that the overgrowth of the egg has resulted in its specialization, but the question still remains, What led to such an over-

* "A Physiological Hypothesis of Heredity and Variation." *American Naturalist*, pp. 85–92, xxiv, 1890.

† Cheshire, "Bees and Bee Keeping," Vol. I, pp. 82–85.

growth of the ovum? This, I believe, may be answered on the supposition already to some extent elaborated that the egg is an abortive attempt at the production of an overgrown spermatogonium which is set free before it has been fully matured, as a result of the precocious determination of superabundance of surplus nutriment to it.

This has been due to forces operating within the parent organism; how, we are still unable to clearly state. If this is so, then the specialization of the egg is accounted for and the expulsion of the polar bodies may be approached from another point of view, namely, that of their morphological equivalence to spermatozoa, since they represent largely the characteristically male plasma in their chromatin. The egg is, therefore, specialized in so far as it is an abortive spermatogonium, and the number of polar bodies, produced as abortive spermatic elements, represent its degree of specialization. The consequent reduction of the chromatin in the egg nucleus may then also be compared with the processes of spermatogenesis in which a certain minimal size of the chromatin mass of the egg is reached, which now makes the ovum the exact homologue of the spermatozoön, but with an enormous cytoplasmic body fitted for the exhibition of active karyokinetic movements and an elaborate series of successive and finally simultaneous karyokineses.

In this way it may be supposed that the peculiar advantages offered for the survival of a species through sexual processes may be realized.* But such advantages were developed not as the result of any foresight, but as a consequence of the action of the principle of overnutrition ending in the production of spermatogonia which failed to segment or break down into male elements before they were freed from the parent. In this way it may be supposed that the ovum itself arose, but that it was a later phase of development than that of the flagellate male germs, which type still prevails in asexual or very primitive forms. This gives us the real grounds for the evolution of the ovum; accounts for its specialization, for the reduction in volume of its chromatin to that of the male element through the expulsion of the polar bodies, through which it also again becomes the immobile overgrown, but exact morphological homologue of the spermatazoön. The specialization which the ovarian egg has attained as an overgrown spermatogonium also makes it certain that the cells expelled as polar bodies represent the energy in part which has been expended, and which is signified by the great size of the ovarian egg. These products of specialized development must be got rid of so that this part of my hypothesis respecting the polar bodies is a necessary corollary of the first part developed in the earlier portion of this paper.

The impulse towards the expulsion of the polar bodies comes from within, upon the advent of an adequate stimulus, and the tendency is to run down towards the male condition from the egg, but such a result is prevented from proceeding far by the small original amount of chromatin in the egg which prevents the formation of more than two cleavages, on the

* "Origin and Meaning of Sex." *Am. Naturalist*, June, 1889, pp. 501–508.

average, when the chromatin is reduced to a volume equivalent to that of the chromatin in a single spermatozoön of the same species. The tendency towards the expulsion of polar bodies is therefore probably self-regulative as soon as a certain minimum in the size of the chromatin masses is attained. The impulse leading to such a result arises from the presence of a large cytoplasmic field sensitive to external stimuli, but in that such a field is cut off from further possibility of growth by detachment from the parent organism and incapable of further growth except through the stimulus of its chromatin, and in that no more of the latter is for the time being elaborated after detachment, it is clear that the cleavages which give rise to the polar bodies are self-limited in number by conditions arising within the egg, and as a consequence of the specialization of the latter as a cell, and in the sense that it differs from primitive types of cells as a consequence of its method of protected growth within the parent.

Why, however, should the polar bodies be so small? Why does not the egg divide equally? This may be answered on the ground already assumed that the chromatin is yet neither male nor female, but tends universally to be reduced to male dimensions even in the egg. The cytoplasm being the most abundant in the egg and the chromatin in the spermatozoön, it is clear that totally different physiological characters must be offered by the two elements. This, in fact, is the essence of the meaning of the term specialization as applied to them, and involves the conception of wide differences in the modes in which physiological energy has worked to produce them, respectively. If the yolk is abundant, the cytoplasm, at one pole of the egg where nuclear cleavage occurs most readily to form the polar bodies, is reduced to a thin layer or disk. This, in many cases, is the condition under which polar bodies are produced so that a great inequality in the size of the cleavage products must result. Later, when the egg nucleus is reduced and can return to a deeper position in the egg, it can gain control of a still larger cytoplasmic field, which is still further enlarged by the advent of a fresh male chromatin and cytoplasmic element. When the male and female elements finally unite there is a complete readjustment of the equilibrium between the cytoplasm and chromatin centres, because the introduced male is capable of taking control of a still larger cytoplasmic field and may even at times overtop the female, as in the case of *Rhynchelmis* described by Vejdowsky. The two together now regain control of the cytoplasmic field of the egg, but cut off from direct dependence upon the parent, so that a new cycle of changes can go on in a new way, and instead of running down towards the male condition, normal segmentation goes on which ends in the formation of a new being under the impulse of the tendencies towards continuous growth under new conditions. The cases of egg and spermatozoön are clearly merely specialized states of chromatin and cytoplasm and their separated and united conditions are merely phases of a continuous process of growth under widely differing conditions which are ushered in as the results, first, of an incipient and complete exclusion from the parent (formation of polar bodies and spermatogenesis), and, secondly, as the results of their union as complementary bodies through which a new development is initiated. Their reciprocal saturation of each other also prevents polyspermy and is self-regulative, just as all of the processes of development will ultimately be found to be, and as we have seen good reason for believing must be the case in respect to the polar bodies.

Finally, on our hypothesis it may be said that the chromatin and cytoplasm in the egg bear a certain proportion to each other, regulated in the ovary. The effort to adjust this relation further after the ovum is free (usually) ends in the expulsion of the polar bodies, which represents an effort at the production of male cells, since the egg as a protovum is invariably the prelude to the production of spermatozoa. The ovum precedes the spermatozoōn in the order of time, and the latter must be produced from the former. Protogyny is, in the widest sense, therefore universal, since it is only ova-like bodies which can break down into spermatozoa in which chromatin preponderates. But this may be further qualified by the statement that protogynous tendencies greatly developed must finally themselves lead to the development of an ovum with a large cytoplasmic field. Or, in other words, a condition is reached in which great cytoplasmic specialization is attained, so that the expulsion of the polar bodies may be regarded as the expiring effort of protogyny to produce spermatozoa.

If this is so, why do not all ova develop parthenogenetically? Simply because these spermatic elements—polar bodies—are not completely matured or developed, and while the transmitted energy of growth is insufficient. The remaining body with its reduced chromatin is now, however, the equivalent of a spermatozoōn but with an enormous cytoplasmic body. It is complementary to the male element in that it is physiologically receptive, and food through karyokinesis for further processes of segmentation. But how about parthenogenetic ova? Why do these develop and why do some of these develop two polar bodies? Here we often, if not always, have, as already supposed, a greater momentum of growth, with frequently a smaller mass, protogyny is not so markedly developed, and the tendency towards maleness and cleavage is therefore inherently greater. If now new relations or rather want of former modes of nutrition of the cytoplasm supervenes after oviposition, the momentum of growth tending to segmentation, received from the parent even after the expulsion of the polar bodies, is still sufficient, so that the so-called female pronucleus is able to proceed under these new conditions to take possession of the cytoplasmic field and initiate normal development under new and independent conditions, through segmentation, leading to the formation of an embryo. If these views are correct, parthenogenesis is the vanishing point of maleness and femaleness, yet, in some cases, its energy is so great that it sometimes, even then, ends in maleness as seen in the development of drones amongst bees, thus illustrating still further the tendency in some cases to run down to the male condition.

If these conclusions will hold universally, there is good ground for believing that in the gradual evolution of protogyny the cytoplasmic field, in which rapidly successive segmentations were possible, was also evolved. If this is true, then sexuality itself arose as the consequence of protogyny starting in parthenogenesis. The primary and secondary sexual characters of multicellular forms were also probably the outgrowth of secondary and adaptive processes consequent upon the effects wrought as here supposed through protogyny and the evolution of a large cytoplasmic field. The origin of sex at any rate hinges upon the decision of how the disproportion between the chromatin and cytoplasm arose in the sexual products of the two sexes respectively. Upon its last analysis this problem must resolve itself into purely physiological factors.

These views are in accord with the first part of this paper, though it may at first seem that the theory that the egg expels polar bodies because of its specialized nature is not well founded. What there is in favor of such a view is, that it harmonizes with the morphological and physiological data of ovogenesis, and the conjugation of Infusoria. In any event, it is certain that if ova represent an incompleted effort to produce spermatozoa, it is very certain that they are specialized in so far as this effort has been realized as supposed, in the formation of polar bodies and a large volume of cytoplasm.

Consequently ova may be regarded as incompletely differentiated spermatogonia. The undoing of this specialization whereby the egg becomes the morphological equivalent of spermatozoön so far as its chromatin is concerned brings us back to essentially the same basis as was followed in the first part of this paper.

Experimental evidence shows that the process of fertilization is self-regulative and restricted to a single spermatozoön. Indeed, one might infer from the evidence of the phenomena of fertilization that such must be the case, and that the ingress of the spermatic element, in sexual forms, is a consequence of the exhaustion of the power of continuous growth, as shown in the abortive effort at spermatogenesis in the extrusion of the polar bodies. A consequence, however, following because of the appetency of the spermatozoön to set up a segmentation in the cytoplasm which should end in a continuation of the process of spermatogenesis set agoing by the expulsion of the polar bodies. Yet, this does not occur, and, as we have seen, a good reason can be assigned why spermatogenesis does not go on indefinitely after being initiated by the extrusion of the polar bodies. Equally good reasons can be assigned why the method of nuclear movement is changed after the entrance of the spermatozoön. On my view this is wholly due to the sudden advent of wholly new conditions, since about the time of the ingress of the spermatozoön the egg is not only cut off from its supply of nutriment and is now an isolated being the whole of the cytoplasmic field of which is at the mercy of the combined action of the pronuclei, while the preparatory equilibrium resulting from the extrusion of the polar bodies has been attained beforehand.

The new external conditions constitute a continuously acting series of stimuli provoking the action and reaction of the chromatin, achromatin, and cytoplasm upon each other, as has been rendered probable by the studies of Boveri and Watase. The isolation of the egg makes it independent; its cleavage products now cohere and the whole plan of its fragmentation depends upon its using every particle of its cytoplasm as reciprocally nutritive material for the maintenance of the integrity of the whole.

Maturation is truly the proper name for the process of the extrusion of polar bodies, and it may be that in some cases the polar bodies may be large enough to merit the name of protova, especially the first one, and that a large enough cytoplasmic field may exist around its nucleus to attract spermatozoa. Yet the polar bodies are nevertheless to be regarded as abortive attempts at the production of spermatozoa.

It may also be that the male condition characterized by the assumption by the elements of that sex of a monad-like flagellate form, is really an attempt at the recapitulation of the most ancient ancestral monadiform condition. In the female we have seen that the attainment of such a condition is abortive, but enough is left in the disguise of the polar bodies to represent a reminiscence of the lowest phase of organic evolution.

We have now recapitulated all the important and difficult queries that have arisen in regard to the meaning of the polar bodies, which we also now see probably have a phylogenetic significance.

The evolution of complicated apparatus and processes for the emission of the sexual products, when mature, is only an accessory and a secondary consequence of the continuous series of processes described above, and which has also proceeded *pari passu* with the divergence in the morphological and physiological characters of the products of the two sexes. The primary sexual characters and probably also the secondary ones have been evolved in response to the all-important requirement of most efficiently disposing of the sexual products. The habit of copulation itself must have so arisen, and the stimulus effecting the discharge of the sexual products finally acts through the sensorium and through the reciprocal contact of the nerve terminations in special dermal tracts concerned in copulation in the two sexes.

In this way it must be supposed that eventually the sexual passion became intensified as the provisions for effecting the union of the sexual cells became more elaborate, and as the parent-body became more and more differentiated and specialized to take a more and more important share in this process. The presence of the germ cells has undoubtedly reacted upon the soma or parent body so as to intensify the tendency towards a greater differentiation of the primary sexual organs, and this through the sensorium and its sensory terminals.

It is interesting to reflect that the tendency to a repression of the male traits in the ovum has been manifested in the adult organization of the two sexes in Metazoa. The assertion of some writers to the effect that the female is merely a retarded stage of the development of the male may be correlated with the singular and suggestive contrasts between the egg and spermatozoön.

The evolution of sex and the evolution of sexual love or passion are inextricably intertwined. The history of the one is the history of the other. There are many reasons leading to the conclusion that the earliest and lower forms of sexuality were never in the past and are not now impelled to conjugate by anything akin to the gratification of passion such as is met with amongst the higher series of animal forms. Sexual passion is the outgrowth of a gradually developed and increased capacity for experiencing pleasurable sensations by the parent body or soma which is the producer or bearer of the sexual products. The high specialization of the sexual processes in higher forms has also unfortunately led to the possibility of their perversion. No sexual perversion is possible amongst lower forms where the essence of sexuality is the mere concrescence or conjugation of sexual cells. Courtship, violence towards and pursuit of the female, sexual love, etc., are the consequences of the evolution of a soma or parent body, which is the mere carrier of germ-cells, but which is capable of experiencing exquisite pleasure in the consummation of the sexual act.

The intromission of an erectile organ covered with highly sensitive nervous end-organs into the genital passages of the female is the appetency for the sexual elements to conjugate reflected upon the soma. Copulation and the development of erectile or other sensitive intromittent and reciprocally coadapted primary sexual organs must have been due to the effect of use, since disuse, as in castration, affects the development of the parts, while abnormal activity, under favorable conditions, is said to increase their development. This view is sustained by the evidence in both plants and animals ; in both the devices for effecting conjugation of the sexual elements and developed in the most gradual manner, until, in plants, the pollen-grains, with the help of various secondary adaptations, such as their morphological development, insect agency, the wind, etc., are evolved into true intromittent organs answering to the function of a penis in the form of a growing pollen-tube, stimulated to growth by nutriment supplied by the stigma and carrying the very minute, elongate, male chromatin element in its very narrow passage to the ovicell of the ovary. In the same way the male intromittent organs of animals have been developed from a mere cloacal papilla, or a low-grooved fleshy erectile process to a highly differentiated and excessively complex penis with, in some cases, an elaborate series of rosettes and flanges covered with a thin integument with highly sensitive terminal sensory nerves, that are in reflex connection with the higher parts of the sensorium and through the lumbar region of the spinal cord with the testes, spermatic vesicles and accelerator urinæ and other muscles which they may throw into spasmodic contractions in order to compress the vesiculæ and cause the emission of the male elements in the act of coition. Similar actions result in the female which affect the peristaltic contraction of the oviducts, the enclosure of the ovary by the fimbriæ leading to conditions favorable to the emission of the egg at the time of coitus.

In animals, the provisions for rendering the male elements more efficient are thus rendered more perfect. There is not wanting evidence that the glans penis mav serve as a sort of piston, fitting closely against the sides of the vaginal passages so as to prevent the regurgitation and loss of the semen. In mice I have observed that in those which have recently been in coitus, the uterus is actually distended with semen. These contrivances, many of which are of the most singular conformation, as that of the pig, for example, probably serve the purpose of more efficiently carrying the seminal matter into the genital passages of the female where they are to subserve the essential purposes of reproduction. At any rate, the wonderful contrivances in the higher plants serving the purpose of efficient fertilization are no more remarkable than those in the higher animals, the study of which has been singularly neglected by physiologists.

In the lowest types of living forms there is nothing which suggests in any way the gratification of passion. The mere tendency towards conjugation of animals and plants without nerves cannot be identified with an appetency arising from any pleasure experienced in such conjugation. There are at first no provisions made for conjugation except such as the accident of contiguity of the conjugating elements as the germinating spores of Myxomycetes, the intracellular spores of *Hydrodictyon*, etc. When the process is so primitive as this, there is no evidence to show that it is anything more than the expression of the cessation of one order of things at the termination of one set of external conditions giving place to a new order of things under the stimulus of a new set of outward conditions more favorable to growth. Under this view of the case the incipiency of conjugative phenomena is simply the expression of a readjustment of the processes of growth under the influence of more or less favorable conditions of life. The physiological traits of that life are expressed in the mode of molecular aggregation and constitution of the cellular unit or units composing the individual. Its tendencies are to increase the mass of the individual by processes of integration of new matter in the course of which such new matter becomes molecularly identical with that of the organism engaged in such integration, a process commonly expressed by the term assimilation.

The consequence of such newer integrations are that still other integrations are possible, under favorable conditions, on a much larger scale than the first ones. The increased power to make continuously more and more extensive and rapid integrations of identical molecules is possibly in some way due to the increase of mass and surface and the consequently increased capacity to liberate energy, or to perform work in a still more active integration and assimilation of molecules.

The Malthusian principle therefore rests, in its last analysis, upon a chemico-physical basis. It is probably, therefore, not an unjustified assumption to state that the acquisition of an increased mass in organic bodies leads to an increased capacity to integrate and assimilate still further additions to the original organized mass, and that if this process could go on indefinitely without the intervention of death and a necessity for oxygen, the earth might be gradually transformed, in so far as its available materials held out for such a purpose, into a few organized individuals. Such a supposition is, however, absurd, since such masses, even were their growth possible, would finally become helplessly immobile from their own weight; such a process would be self-destructive and incapable of indefinite maintenance.

If, however, the principle that successive increments in the mass of organized bodies, carries with it the implication that such increments imply their capacity to increase more and more rapidly, under favorable conditions, or as it may otherwise be expressed, are thus enabled to grow, in virtue of such an inherent property, far beyond the bulk of their original germinal mass, then this deduction must form the basis upon which the phenomena of growth, reproduction and sex must finally be interpreted. This principle affords also the physico-chemical or physiological reason for the foundation of the Malthusian principle that the production of organisms would if unchecked outrun the available food production for a certain section of such organisms, as an aggregate—namely, the animal world.

The foundation of the principle of Malthus and of the Darwinian principle founded upon it, therefore lies within the domain of ultimate biological physics or the molecular dynamics of organized bodies. The mainspring of the principle of natural selection, upon final analysis is not itself a choice between two things but an inevitable consequence of the innate molecular habit of living matter, if I may so express myself. It is physical in that the chemical and physiological laws under which growth or molecular integration can take place are themselves resolvable into physical laws which can be coördinated under the principle of the conservation of energy.

This physical principle of continuous and continuously augmented integration and the consequent increase of the mass of living bodies is the primary conditioning factor of growth by intussusception of similar molecules. It initiates the struggle for existence, as the struggle due to motion and the attraction of stellar bodies, maintains the latter in their harmonious relations in space.

This principle must, however, be further qualified in that the properties of the molecular integrating factors of living organisms differ very widely. Some forms (vegetal) under one set of conditions can integrate new and more complex assimilable molecules by recombining binary compounds; other forms—animals—can assimilate only such new ternary molecules or such as are very nearly similar to their own, while a third form, the sexual, is probably the highest expression of this integration of similar molecules in that here the molecular differences are zero or nearly so, and at most goes no further than molecular differences, having their origin in the individual traits of either of the two parents. The last or sexual form of integration or intussusception also occurs, *en masse*, and without any reciprocal sacrifice of molecular identity. This last form of organic molecular integration is therefore effected with the least expenditure of energy on the part of the sexual elements themselves which are involved. Sexuality according to this view as expressed primarily in conjugation is a sort of refined hunger, in which neither the "eating" nor the "eaten" expends but a minimum of energy in a process of reciprocal assimilation. It is a hunger in which the sense of "taste" in the vulgar, anthropomorphic sense is unknown ; it is an affinity developed possibly through the attraction of identical molecular aggregates for each other.

The principle of cumulative molecular integration is similar in some respects to the cumulative principle operative in organic structural evolution, through which a superposition of adaptations results, not necessarily as the consequence of selection but as the result of the morphological and physiological necessity of conforming in the next step of morphological and physiological complication to that which had preceded it. Many instances in illustration might be cited, such as the annular placenta of the ovum necessarily conforming to the easiest possibility of internal contact with a tubular uterine canal. This principle has been responsible for much that has happened in organic evolution, but it is again dependent in curious, circuitous ways upon the still more primary principle of cumulative integration, overgrowth of organisms, or their capacity to grow beyond their own bulk at certain points, as implied by Haeckel.

The highest form of cumulative integration ending in an overgrown and abortive spermatogonium, which is the equivalent of the egg, together with its further expression in the production of spermatozoa which have had their cytoplasmic field reduced, leads to a condition where the one becomes helpless without the other. It also presumably leads to the evolution of an appetency or affinity of the male for the female element in that the one possesses what the other does not, and in that they are produced in similar organisms or those of the same species their idioplasmic constitution must be very nearly the same, except for the morphological differences which characterize them. These differences are again the preponderance of nucleoplasm in the one or the element immediately concerned in growth and the physiological integrity of the living cell, and the preponderance of cytoplasm in the other, which is the medium in which free nuclear motion, karyokinesis, and consequent growth is possible. The affinity so developed through cumulative integration by the divergent processes of ovogenesis and spermatogenesis ends in what I shall term *reciprocal integration* without loss of molecular identity, or in what is usually termed "fertilization."

The advantages offered by such a process is that it provides for the development of metazoan or multicellular embryo, which is without the need of immediately feeding, but which is enabled to reach a certain self-helpful morphological complication before it begins the struggle for existence for itself. It provides a large cytoplasmic field in which rapidly recurrent successive and simultaneous karyokineses can take place under the guidance of the inherited tendencies resident in the nucleoplasm and cytoplasm of the combined germs. The one sex appears to supply the field for segmentational activity, the other the segmentational impulse itself. In other words, sexuality is the expression of the action of the principle of the physiological division of labor, extended so as to involve two kinds of individuals of the same species, or two different functionless parts of the same individual, as in hermaphrodites.

There is no convincing evidence that the male induces variability. The argument from hybrids is of little value. The tendency to an equilibrium as the consequence of close interbreeding or of continued promiscuous interbreeding is the same, and is to be interpreted as the result of the constancy of the mode of growth of the average individual which must finally result, following from the average of hereditary characters which are finally thus transmissible. As soon as slightly differing forms are crossed the karyokinetic equilibrium is disturbed and variability ought on *a priori* grounds to ensue. To saddle the induction of variability upon the male does not seem to be demonstrated, as the factors involved are too numerous to enable us to decide what ones are important and what are unimportant.

A view which has far more in its favor is that a large oösperm, interpreted as above, with a large cytoplasmic field, is inherently more liable to vary its karyokinetic processes through very slight variations in the external influences than a small or a parthenogenetic one. That sexuality, taken in the widest sense, is responsible for variability is probably nearer the truth. That the oösperm, with its large cytoplasmic field, is the real arena in which variability disports itself, may be taken for granted. It is also very evident that the evidence derived from the development of monsters is clearly in favor of such a view. Monsters are developed only when the early stages of development are karyokinetically disturbed, as is well known. Moreover, there is no hard and fast line between monstrosities and variations of a less and less monstrous character until those of an almost imperceptible and unimportant character are encountered. That the tendency towards variability is more marked in the young than in the adult stages of fixed and slightly variable types of Metazoa may be regarded as a truism, and must be considered the foundation of these views.

In that temperature affects the rate of karyokinetic processes, it is clear that inequalities of temperature simultaneously affecting different points on the surface of an egg would affect the rate of segmentation of the cells of such different points and thus induce variability. A single karyokinesis disturbed or impeded on one side of an embryo must disturb all subsequent ones. A mechanism so delicate as this of karyokinesis may also be interfered with in other ways. It seems almost self-evident that where karyokineses become simultaneous and rapidly successive there must be a greater inherent probability that variations should be induced through disturbances of the karyokinetic processes.

Latterly much discussion has taken place regarding rejuvenescence and the relation of the process of fertilization to a supposed renewal of the youth of the sexual cells. It may be suggested that the sexual cells probably never grow old from the causes which act upon the other cells of the body to render them senile, and it may be that the real ground for a theory of rejuvenescence lies not in fertilization itself but in the fact that the sexual cells are functionless and have not been belabored with physiological duties in the parent body. Where they are produced annually, as in many animals and in all plants, they are also the youngest cells of the parent body, while the spermatozoa, produced in some animals at hourly intervals, are still younger, or more youthful. The male cell is therefore the most youthful, the least functional and the one most disposed to exhibit its activities of growth under favorable conditions with the greatest energy, though not necessarily in the sense that such a display of greater energy would be favorable towards provoking variability, except as provided for by the cytoplasmic field of the ovum or female element.

It has also been pointed out that the first cleavage of the oösperm corresponds to the future median plane of the embryo or to the line dividing the future hypoblast from the epiblast. But there are still other relations which connect these phenomena with the fore and aft disposition of the body of the parent. It is a matter of common knowledge that the Infusoria when undergoing division divide either lengthwise or crosswise. In fixed forms—*Vorticella*—the division occurs lengthwise of the parent and in conformity to the mode in which the future individual is related to the colony by its base. In many free forms the division is crosswise, and it is a singular fact that the end of the hinder individual next to the posterior end of the anterior one becomes the future anterior end of the hindmost one. These two forms of division have been developed adaptively and in conformity with very different conditions in the two cases. Why should the end of the young Paramœcium next the foremost or parent individual become its anterior extremity preferably to the other one? Does this not indicate that use and habit may have had an influence in giving the plasma of both a bias which extended to the soma of the posterior bud and which expresses itself in this peculiar polar conformity to that of the anterior parent individual, which is more somatic in its character?

Numerous other forms, such as *Volvox*, illustrate the same tendency of the axis of the young to conform to the axis of the parent. In Fishes the embryos of *Batrachus tau*, which are attached to a fixed substratum after the rupture of the egg-membrane, by the adhesion of the yolk sack to the latter, show that, at the time of deposit, *the future axis of the whole brood of embryos was predetermined in the body of the parent.* That this must be so may be concluded from the astonishing fact that the heads and tails of a whole brood conform in direction, within a degree or two, to a common axial plane. How was such an astonishing conformity to a common axis brought about, if it was not developed in the ovary of the parent before oviposition? If this is true then the axis of the parent and the polarity of her body, as expressed in its fore and aft extension, exerted such an influence upon the brood as to impress such a polar tendency, and transmit it directly to every egg matured in her body. If this is true, then the parent body does transmit characters directly to its offspring, Weismann, Lankester and other deluded skeptics to the contrary notwithstanding. Here is a whole brood of young fishes, fixed to the surface upon which they were hatched, every one of which conforms, to within a degree or two, to lines running parallel to each other in a common direction. Does or does not either parent transmit this; since one or the other must do so, how is it done, and why is this not proof that the soma of the parent transmits certain polarities, and those of the most important character, directly to the germ-plasma from which the embryos are developed? The case here is just as clear as in the case of Vorticella or Paramœcium; they are in exact conformity, so that we have here once more direct evidence of the untenability and absolute falsity of some of Weismann's deductions as to the non-transmissibility of acquired characters.

In a similar way, how is the polar conformity of the chick in the egg to the axis of the parent bird to be accounted for? Though in this case the axis of the embryo lies constantly at right angles to that of the parent as the ovum descends through the oviduct. Equally striking are the constant relations of the embryo Rabbit, in the uterus up to the tenth or twelfth day, at right angles to the axis of the parent body. The same is true of the Cat, Dog, Mouse, Rat, and other forms. The same principle also holds in Arthropods, where egg-tubes are formed and where there are also constant anterior and posterior poles of the eggs developed, which bear a constant relation to those of the parent. Here are bodily habits directly transmitted which involve nothing like a change of structure; does the germ-plasma accomplish this, or does the direct influence of the mother's organism accomplish this remarkable result? For me the latter alternative seems to be the only explanation.

Similarly the phenomena of budding in Salpa, as worked out by Brooks and Seeliger, tend to establish the same conclusion, namely, that the polarities of the immediate parent influence those of the offspring directly. It looks as if the bodily functions of the parent either impressed themselves as if from a distance, or through the pole of the germ most directly in a nutritive relation to the parent upon the still unconscious germinal matter giving it these tendencies to conform in these curious ways to the polarities of the parent organism. It is also tolerably clear that the so-called "promorphology" of the egg is preceded by a still earlier morphological history, which has been scarcely more than touched by students of the Metazoa. The direct influence of the source of the nutriment supplied to the growing embryos is probably indicated in these singular examples, no less than in the fact that the polarity of young, viviparously developed aphides corresponds to the fore and aft polarities of the parents. Or, as in the case of the ovarian leaflets of the ovary of the lamprey, the micropyles are found to be invariably turned towards the vascular core of the leaflets, and consequently towards the sources of nutriment and oxygen. In this last case also, these factors have determined the position of the future germinal or animal pole, and consequently the point on the egg where development shall begin.

The points which have thus far been elaborated tend, in a general way, to support the conclusion that, in the production of ova and spermatozoa, both have arisen from a common basis. The lowest forms, we certainly know, tend to multiply without attendant karyokinetic processes, probably, as suggested, because a cytoplasmic field or arena in which nuclear movement is possible, is wanting. In the lowest Monads sporulation results in the breaking up of the parent body into infinitesimally minute germs, which are, presumably, composed in the main of chromatin or nucleoplasm, a conclusion which comports with the fact now ascertained, that the chromatin or nucleoplasm of lower forms, if deprived of its envelope of cytoplasm, may regenerate it. Overgrowth of mass, so as to form a large cell-body composed of cytoplasm, is unknown amongst the very lowest forms, which are also flagellate. In the next step (*Nostoc*), the overgrowth of certain cells means that they are incapable of development. In the next step, the conjugation of overgrown cells, with those in which nucleoplasm preponderates, restores the power of growth or the power to integrate cytoplasm anew, or, as in Infusoria, conjugation stimulates the production of nucleoplasm through the constructive metabolism of the investing cytoplasm.

All of this evidence tends to prove that maleness, or the condition of the flagellate spore, is the primitive one as already stated. Since the very lowest animal forms are likely to preserve some reminiscence of the primitive processes leading up to animal sexuality in its most generalized form, it will be desirable to appeal to the evidence offered by such forms. The Amœba is undoubtedly animal in nature, but notwithstanding the persistence and frequency with which it has been studied, much still remains to be learned of its life history.

Leidy has shown that, in certain forms of Amœba, the nuclei tend to multiply after reaching a certain size, and through a tripartite division without karyokinesis. One of these nuclei is then transported to near the surface, where it bursts and allows the balls of chromatin adherent to its walls to escape into the surrounding water, presumably as germs, but he did not trace their history. If this should prove to be a true case of sporulation, it would prove that in the Amœba there are conditions which favor the production of chromatin, and that the germinal matter or nucleoplasm is "set aside" in the nucleus from which it is expelled.

Mrs. Lillie Holman's observations (*l. c. supra*) also tend to show that a conjugation may occur where one Amœba swallows another and then disgorges it. The disgorged one then comes to rest and becomes encysted; it then discharges upwards of two hundred spores, since the further results of the development of the latter were observed the next day in the same "life-slide" as very minute young Amœbæ.

Brass* has given a more circumstantial account. According to him the body of the Amœba after encystment undergoes at least superficial subdivision into cells. The cyst then bursts or opens at one point and these superficial cells escape from the cyst as minute flagellate monads, which soon lose their flagella, becoming at the same time again amœboid and settle upon objects over which they creep about as did their parent, of which they are a fragment. They now also feed very actively, grow rapidly and soon become the counterparts of the parental organism, which gave rise to them by fragmentation. A somewhat similar history has been worked out by Haeckel for *Protomyxa*, and Weldon has reported the detachment or escape of small germs from the body of *Pelomyxa*.

We have the spermatogonium typified in this peculiar method of fragmentation of the Amœba, especially as described by Brass. It is an overgrown cell breaking down in part, but first elaborating more chromatin, just as a spermatogonium does. The overgrowth in mass of the parent cell is due to cumulative integration. The flagellate offspring represents the spermatozoa produced by a spermatogonium in a multicellular form, but with this difference that a spermatozoön cannot withdraw its flagellum and begin to feed. Such a flagellate germ of a higher multicellular form must then perish if it is not nourished in some other way. The only way in which it can be nourished is to blend with the cytoplasmic body of another abortive but hypertrophied spermatozoön—the ovum, as supposed above. In other cases, mammals and birds, it is known that the spermatozoa or flagellate germs of the male die if not kept at the same temperature as the parent body. They are not adapted to continue to live in the cold medium in which the flagellate germs of an Amœba would at once begin to feed and grow.

The flagellate or wandering germs of the Amœba are wandering in habit, probably because they inherit an organization favorable to vagrancy from still lower monad-like creatures. And this wandering habit is doubtless advantageous to the young Amœba, as they are thereby scattered so as to be placed where food is more plentiful, at any rate, the offspring of one parent Amœba do not, as a consequence, fall into a heap at one place so as to come into such close competition with one another for food.

Such vagrant habits would be of advantage to the germs of almost any species and they are certainly of use in many cases in that they favor the distribution of a species. In the case of the male germs of higher, in fact, of all forms, this vagrant habit becomes useful in effecting their distribution, and at last of aiding them to find the egg and the micropyle, if such is developed, through which they enter the ovum. So that here again we find that a habit which has at first thought apparently no preëminent

* "Die Zelle, das Element der Organischen Welt," pp. 63–65, Thiéme, Leipzig, 1889.

value or importance in the very highest forms, but which has such an importance in lower ones, may serve a very different purpose in higher types, that is, to find the female element so as to combine with it, which, of course, would be an advantage to the species. In this example, we find an illustration of change of function, or rather the use of an old function in a new way, illustrating also the principle that, any further advantageous step in evolution avails itself of the service of the next preceding one in the order of time, or rather, the latter is apt to thus become a stepping-stone to farther progress, as is shown in this instance.

The parallelism of the Amœba before breaking up into flagellate germs, with a spermatogonium in a higher form is, however, complete, and it is from this basis that further criticisms and suggestions may now proceed.

Geddes and Thomson, in their suggestive work on sex,* have attempted to identify the evolution of the female germ or ovum with a tendency to develop a leaning towards constructive metabolism or anabolism, while the male germ exhibits the reverse tendency or towards destructive metabolism or katabolism. So far as the directly palpable facts are concerned which lie upon the surface, these conclusions of Geddes and Thomson would seem to be justified. There is apparently nothing in them which conflicts, at first thought, with the facts of morphology and physiology. Yet, I believe that the prime conclusion of these authors is capable of further analysis, and consequently that it is not as important as it appears to them, nor is it strictly and entirely true in a physiological sense.

The growth of an egg we will admit requires constructive metabolism to extend over a longer period than if the germ were male. While it is true that growth represents the expenditure of a certain amount of energy in the form of metabolism, it is by no means clear that the energy of growth required to produce a number of male elements equal in volume to an egg is any greater in the one case than in the other. It may be said that there must necessarily be more cell divisions or karyokineses in the case of a given volume of male elements than in the female, but this goes for nothing in that it cannot be shown that the metabolism or energy expended in building up and segmenting the one is any greater reckoning the additional and usual formation of an egg membrane in the egg (which is wanting in the other element), than in building up the large mass of plasma in the ovum. But in some eggs there is no egg membrane. Even then the process of spermatogenesis is not strictly to be compared with a disruptive metabolism or katabolism; on the contrary, as an end product of cytoplasmic activity, the male cell is in the main the highest achievement of constructive metabolism as represented in its preponderant nucleoplasm. The lowest forms of life have apparently a greater capacity for the development of nucleoplasm or chromatin-like substance, than the cells of higher animals, but even there, as in higher forms, there is the best evidence that the cytoplasm is the real agent in the production of the nucleoplasm; the latter grows, as we know, at the expense of the former.

* "The Evolution of Sex," New York, 1890.

The processes of metabolism, it is true, are carried a stage further in the production of flagellate germs and male elements than in the female, but it is not towards a lower plane of molecular structure, but towards a higher one than in the female germ. It may be said that metabolism is controlled by the nucleoplasm or chromatin, in that the volume of the one increases with the volume of the other as in a growing Amœba. An insufficiency of nucleoplasm would render a cell inert and incapable of coördinating its large cytoplasmic field, as experiment seems to demonstrate. The continuous processes of growth therefore ending in the expulsion of the polar bodies bring about such a stage of cytoplasmic inertia, in which the process of fertilization and the concomitant access of a highly complex and anabolic male element would restore the balance between the cytoplasm and the nucleoplasm. The "katabolic tendency" of the male element is more apparent than real; it has a greater capacity for katabolic change than the female as measured by the relative volume of its nucleoplasm, but absolutely it has far less because of its small size as compared with the whole ovum. The question of the genesis of sex is not to be disposed of in quite so simple a way as is done by Geddes and Thomson, or in a sentence. These authors have missed the essence of the matter in that they have not noted the essential distinction which exists between the egg and the spermatazoön, nor the transcendant importance of the process of cumulative integration. The cytoplasm preponderates in the one, while the nucleoplasm preponderates in the other. No reason for this has been assigned by these authors. Is not the evolution of a larger amount of nucleoplasm than is contained in the egg, as must happen were it to break up into spermatozoa expressive rather of preponderant anabolism than of preponderant katabolism? Is also the greater mobility of the male element an expression of a specially katabolic tendency? Is not its mobility due to an inherited tendency in part, derived from its most remote flagellate ancestor, and partly to its small size, form, mode of genesis and molecular structure?

The contrast between the modes of production of the male and female elements in *Ostrea edulis* is typical. The difference appears to lie *solely* in the fact that, in the case of the egg, the *whole* of the overgrown spermatogonium is expelled, but is not a mature ovum until after the expulsion of the polar bodies; in the expulsion of the male elements only a *part* of the spermatogonium is expelled, this process being accompanied beforehand by the elaboration of an excessive amount of chromatin by the mother nucleus of the spermatogonium, this chromatin serving to form, in the main, the nuclei of the multitudes of spermatozoa so set free. In that the chromatin used in the development of spermatozoa is formed at the expense of the cell body of the spermatogonium, there is an almost exact equivalence in the plasma that remains as the cell body of the ovum, so far as the metabolism expended in its production is concerned. The essential difference seems to me to lie not so much in any supposed diatheses which are more or less anabolic as in a difference in the functional properties of the plasma of egg and sperm, developed as a consequence of the physiological division of labor in the cell between cytoplasm and chromatin. The former is the immediate agent of intussusception, the latter controls and coördinates the processes of the former. The one is produced in a confined place tending to repress segmentational activity or nearer abundant supplies of nutriment. The other is produced in open cavities which admit of the free escape of sex products, or in regions, or at times when the determination of pabulum is less abundant than in the case of ova. Looking over the arrangement of the reproductive organs and their relation and proximity to the nutritive system, in many forms these views will be found to have much evidence in their favor. Nevertheless there is no evidence in favor of the one process being more katabolic than the other. They are equivalent, only that in the ovum there is a repressed segmentational tendency, in the spermatogonium an unrepressed one. The tendencies are towards the male or primitive monadiform condition in both, only that secondary physiological influences are repressive in the female and irrepressive in the case of the male element. Segmentation into spermatozoa is hindered in the egg, favored in the case of the spermatogonium. Yet despite this there is not the slightest evidence that the results in the two cases are not equivalent so far as the expenditure of energy is concerned.

The real difference in the result lies in this, that in the female element there is an enormous cytoplasmic field in which simultaneous and successive nuclear movement can take place leading to the realization of a coherent process of development instead of an incoherent one such as occurs in the breaking down of the spermatogonium into spermatozoa. The process in the one case is cohesive, in the other disruptive and self-destructive. The tendency then in the female is towards morphological integration, in the male towards morphological disintegration, but upon the common basis of the spermatogonium.

The real gain of this is not in the absolute bulk of the embryo simply, but in that such an embryo may become self-mobile and self-helpful in spite of its size. Herein lies the true significance of sex and of the cumulative process initiated through the repression of the primitive segmentational tendency of the spermatogonium. An embryo thus developed can go through an entire and elaborate cycle of embryonic development without requiring to take food at all and attain to a self-helpful, self-mobile condition.

It is therefore obvious that in such a process of repression of segmentation of the spermatogonium there has been a distinct advantage gained in the struggle for existence, in that such a spermatogonium could directly become the means by which a rapid or saltatory process of evolution could be accomplished, resulting in the evolution of larval forms. From such a stepping-stone the hypertrophied spermatogonium—ovum—other advances were possible, especially in the direction of variation, since such rapid simultaneous and successive segmentations would provide the most extensive possibilities for variation. This must be true upon the simple ground of the theory of permutations, since every cell added to the aggregate of a segmenting germ must increase its capacity to vary. This gives not simply a capacity to vary as if variation were fortuitous, but as a consequence a capacity of adaptation which is proportionately and demonstrably greater during their earlier stages, a circumstance again in conformity with the fact that all living metazoan types have diverged directly from the ovum, as is proved by their ontogeny.

The reproductive cells, as stated in a previous paper by the writer,* are functionless, so far as being of any service to the parent body producing them is concerned. The only function they have in relation to the parent body, is to lead a pseudo-parasitic existence at the expense of the surplus nutriment elaborated by the parent organism ; but these pseudo-parasitic generative cells are themselves the products of the continuation of the processes of cellular growth and fission of the parent plasma.

Being functionless, the reproductive cells of both sexes also tend to revert to the most primitive form of reproduction, namely, to break down into spores, as illustrated by the bodily fragmentation of the majority of lower forms into spores, or the multiplication of the nuclei of some of these forms at the expense of their cytoplasm.

In the male this reversion and breaking down into spores is most complete in the evolution of a spermatogonium, in the female it is incomplete in that the reproductive cells are in some way prevented from breaking down either by excess of nutriment or proximity to nutriment under enclosed or encysted conditions, which tends to be overcome at about the time the eggs are set free or after that time, as expressed in the expulsion of the polar bodies. The female individual may therefore be regarded in the light of a male organism in which the excessive tendency to sporulation has been repressed or retarded. The female state of all higher forms may be regarded as a suppressed or retarded male condition.

This repression of the male condition within the parent body leads however to a process of cumulative growth in the ovary or female gonad which expresses itself as the continued increase of the volume of the spermatogonium, leading to the evolution of a large amount of cytoplasm. After detachment of the hypertrophied spermatogonium, as an ovum, the source of supply in the form of nutriment is cut off, and whatever karyokinesis now goes on must proceed at the cost of a small amount of nucleoplasm, which soon exhausts itself so far as any exhibition of the energy of growth is concerned in the production of the polar bodies. After the expulsion of the polar bodies the egg is probably able merely to so adjust its internal forces so as to prevent the ovum from disintegrating.

In this condition the egg is incapable of further growth and in that the spermatic body from a fully developed spermatogonium, developed in the male is alone capable of reinforcing the exhausted female nucleus, so as to let loose the potential energy, for the time being, stably locked up in

* "Origin and Meaning of Sex," *Amer. Nat.*, 1889, pp. 501–508.

the cytoplasm or cytoplasm and yolk of the hypertrophied female spermatogonium or ovum, it must have access to the latter.

The egg before the expulsion of the polar bodies is a spermatogonium, after that and exclusive of the polar bodies it is the exact homologue of the spermatozoön in that its nucleoplasm is now reduced to the volume of the nucleoplasm of the male element of the same species.

The male spore is however so specialized as an organism in nearly all forms that it is incapable of nourishing itself. Clearly, the only way it can do so is to find lodgment in a body whose molecular constitution is as nearly as possible similar to itself, otherwise its identity must perish in that it would either be digested or in some way absorbed, neither of which fates befall it in the egg, as we know from observation. That body in which it can find lodgment is the female spore or germ of its own species, in which it is not only not digested but is taken in as a partner literally, since it completely fuses with the female centre of control hitherto coördinating and maintaining the integrity of the cytoplasm.

But as soon as this fusion of the starved spore—male element—and the overgrown female element happens, the further changes which now take place must proceed in the presence of the stimulus of abundant nutriment (represented by the cytoplasm of the egg) for the male; but this is not all, the egg is now detached and cannot be nourished for a time, and its career of development is now also profoundly influenced by such all important new conditions as the surrounding oxygen affords for renewed metabolism, under the new free condition, all of which taken together makes for a tendency towards a new mode segmentation which tends to recapitulate the growth of the parent form.

The process of fertilization is probably more like one in which there is a reciprocal blending of two living bodies in which there is no loss of identity of either in that their essential molecular constitution is exceedingly similar. Reciprocal digestion does not occur since the organization of both germs would be sacrificed if such a process were to occur. So far from that the organization of both germs is in a sense maintained, and we have in the blending of male and female elements the paradox of two cells becoming one without the sacrifice of organization in either during the process of fusion. It is therefore manifest that the application of the term mutual or reciprocal digestion as attempted by Rolph and maintained by Geddes is wide of the mark and not descriptive of the process at all. "Fertilization" is really the highest and most specialized form of molecular integration, and is itself the highest phase, and a consequence of the universal principle of cumulative integration, which underlies all continuous growth which in turn must end, on account of the requirements demanded by the surroundings, in discontinuous growth, the production of unlike germs by the same species, and consequently in sexuality.*

* The theory of the polar bodies developed in this paper remains to be put to the test. I find that the nuclei of the spermatozoa of *Ostrea edulis* take up the methyl green while the nuclei of the spermatogonia take up the saffranin from a solution of those two dyes

The causes of the "setting aside" of the "germ-plasma have acted directly and in an adaptive manner." "Nature is no spendthrift but takes the shortest way to her ends." Weismann assumes that the reproductive cells are "set aside" as the consequence of the action of the principle of the physiological division of labor. The cause of the physiological division of labor he attributes to the "action" of "natural selection." Is this true?

Taking one of the lowest forms of reproductive activity as illustrated in *Volvox* we find that the germ-cells are not yet constantly or definitely localized except that we may say that they arise in the posterior hemisphere of the colony. Examining *Volvox* from the standpoint which recent knowledge has afforded, it is clear that the anterior pole is differentiated to a degree not attained by the posterior pole. This differentiation clearly stands in a definite relation to the greater action of the light on the anterior pole from the germinal condition onwards through life. It also stands in a definite relation to the differentiation of the anterior pole as the directive and phototaxic one in the course of the execution of the motions of the whole organism rotating on a definite axis.

Furthermore, the organism when at rest, as it frequently is at the surface of the water, has the upper pole turned towards the light, and under these circumstances is it not to be supposed that the lower pole, which is the heavier on account of the presence of the large germs, would gravitate into its inferior position? I do not see how such an admission is to be avoided. If this is so the tendency once begun would tend to be intensified, since those peripheral cells which began to be receptive to the surplus nutriment elaborated by the whole organism would tend to maintain that tendency and the heavier they grew the more constantly they would tend to turn the anterior pole, where the largest "eye spots" are found upward towards the light. This would give the light an opportunity to maintain the specialization of the anterior pole as the photophilous one, and thus intensify its phototaxic tendencies.

The anterior pole would then be most active in its reactions to light, the posterior one least so as is actually the case. The evolution of the physiological differentiation of *Volvox* can therefore be directly traced to the action of the principle of overgrowth or overnutrition reacting under the influence of gravity upon the equilibrium of the colony so to adjust it that the colony will be uniformly acted upon generation after generation in the same way upon the upper pole. This would be an all-sufficient cause of the physiological differentiation or the real cause of the physiological

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mixed together. Balbiani has obtained somewhat similar results with the testes of Elasmobranchs and Mammals, using picrocarmine and methyl green. If the polar cells are abortive male elements they should have a greater affinity for methyl green than the female pronucleus. If such results were secured my hypothesis would obtain microchemical verification. Indeed, I am inclined to think that the fact which I have observed, that the one pole of the dumb-bell-shaped chromatin mass in the nucleus of the immature egg of *Ostrea* stains with methyl green, while the other pole stains with saffranin is distinctly in favor of my interpretation.

division of labor observed. This process of morphological specialization in *Volvox* is therefore not necessarily due to natural selection alone.

There are still other reasons why the physiological specializations in *Volvox* have proceeded along the lines they have. It may be asked why the germ-cells tend to bulge inwards as they enlarge into the jelly which fills the cavity of the colonial sphere. Why do they not bulge outwards?

To this it may be replied that light, oxygen and food react from the exterior of the colony. The mobile protoplasm through which supplies of nutriment come, must be most exterior. The katabolic running down of the accumulated nutriment matters into less mobile coarse granules which need and consume less oxygen, requires that these materials shall be pushed inwards where they will not obstruct respiration.

In this way, upon the ground of physiological anatomy and the reaction of the incident surrounding forces, the process of the "setting aside of the germ-plasma" in *Volvox* can be fully accounted for without appealing for an instant to natural selection. There is clearly nothing further needed.

It might be said that "natural selection" would favor only those individuals which did not have the germ-cells bulging outwards, because they could not so conveniently rotate or move forwards. Yes, but *Volvox* does not, in the first place, continuously rotate. In the next place, even if "natural selection" did work the wonders claimed for it, it is clear that the explanation here suggested is one which involves no waste of the forces of growth or of individuals, but is operative in virtue of the continuity of the processes of growth, besides it meets the requirements equally well with the hypothesis of natural selection.

The natural selectionist will next appeal to the morphology of *Volvox* in some other direction and ask, How was the hollow sphere evolved? This, in its turn, is clearly and purely adaptive. The growth of the original colonies, which were doubtless evolved from such as broke down into planogametes, grew directly into larger multicellular aggregates which would directly arrange their cells so as to derive the greatest advantage from the surroundings and in attaining that adjustment, the globular form was assumed, in that it offered the maximum opportunity for oxygen, food, etc., in the form of a hollow sphere with the gametes joined by protoplasmic bonds. The selection of the pattern of the form of the whole organism is thus traced to internal forces acting in direct response to outer conditions and not as the result of a murderous process of "selection" and "survival of the fittest." *

But this is not all, if the argument applied to the driving inward of the

*The method of segmentation itself must be regarded as a necessary adjustment of the cleavage planes in such wise, as to divide the large globular ovi-cells into approximately equal parts continuously. An adjustment of this sort effects the equal reduction of all the cells resulting from segmentation, and keeps them below a dimension or mass which outruns the surface to an extreme degree, since according to the Leuckart-Spencer principle beyond a dimension of six, mass begins to rapidly exceed surface and bring about conditions unfavorable for respiration and metabolism.

accumulated products of assimilation in order to avoid the peripheral obstruction of respiration the same argument can be applied to the localization of the germinal matter at the posterior pole. Suppose an ancestral Volvocine form still in a condition when it had not yet began to permanently cohere into a spherical colony. Suppose further; that when its maximum dimensions of growth had been nearly attained all its cells were so nearly alike that the differences would be extremely slight between them. But suppose them to be even very slightly different enough in size to respond to an equilibration of the colony by gravity at the surface of a still pool on a quiet sunny day. The upper cells would undoubtedly be stimulated into a slightly greater assimilative activity than the lower ones away from the light and shaded by the upper ones. The assimilated materials would not only be repelled towards the lower pole by this activity of the protoplasm of the upper pole, but would actually gravitate towards that pole. We thus see that, analyze the physiological data in whatever manner we please, there finally remains no warrant for the hypothesis that the germ-plasma is set aside in special cells for the express object of maintaining the continuity of the processes of reproduction. This apparent setting aside of germinal matter is itself the consequence of the necessary mode of the correlated action of physical agencies, ending in cumulative integration through continuous growth, and is clearly not the result of any elaborate selective process.

The running down katabolically of some of the assimilated or stored germinal matter is proof of its loss of function and uselessness to the parent organism except in so far as such cells are a repository for such materials. There is therefore no conclusion open to us but that one which assumes that the motive force of all these elaborate correlations in such a simple multicellular organism * are the results of the indirect action under cosmical conditions, of the principle that living matter tends to increase in bulk beyond the actual physiological requirements of its secular existence.

Summary of Conclusions.

1. Cumulative integration or assimilation beyond the current needs of the parent organism seems to have arisen as a consequence of the physical properties of "living" matter, as manifested in metabolism or the characteristic continuous disintegration and integration of such matter. It is a property of "living" matter which is a consequence of its molecular constitution; if so, "living" and the continuity of molecular change through metabolism is a physical process, differing only from ordinary chemical processes in its complexity, continuity and capability of self-maintenance under certain conditions; its most important consequence is continuous growth.

* The researches of Overton and myself have proved beyond doubt that Volvox is not a protozoön or protophyte as erroneously supposed by Lankester and Bütschli.

2. The law pointed out by Leuckart and Spencer that beyond the sixth dimension above unity mass outruns surface, may be regarded as in some way operative in hindering the growth of cells, through cumulative integration, beyond certain dimensions, in order that they may carry on respiration, nutrition, in a word, metabolism, most efficiently, under ordinary cosmical conditions. The average of cellular dimensions varies in different forms. So does the molecular constitution of living matter, giving rise to idioplasms.

3. The continuity of growth is maintained through cumulative integration, the continuous reduction in mass of "living" matter is effected through segmentation in some self-regulated way, presumably according to the Leuckart-Spencer principle.

4. The growth of the lowest forms of living beings is effected in the main or ends principally in the production of a single kind of living matter. In higher forms, in which the cells are also generally much larger, two kinds of living matter are developed in very unequal proportions. In the first case when division occurs, due to growth, there is little or no reaction between the two kinds of living cellular substance and division is direct or without karyokinesis. In the second case there is a reaction between the two kinds of living matter which is expressed most strongly as karyokinesis, or nuclear motion on the one hand and the development of fibres on the other radiating from or converging upon the nucleus.

5. The effect of cumulative growth of the cell-mass has been to finally produce a preponderating quantity of plasma which invests the primitive nuclear plasma or chromatin with a thick envelope; this envelope is known as the cell-body or cytoplasm, and also provides a *field* or space in which the action and reaction of the two kinds of living matter found in the cells of higher forms may display itself as karyokinesis. The plasmic space in which this occurs may be called a *cytoplasmic field.*

6. The action and reaction between the two kinds of plasma controls the order and direction in which the phenomena of growth take place, but in conformity to certain dimensions and earlier relations of the cytoplasmic field to its sources of nourishment.

7. The effect of the forces at work in cumulative integration is to augment mass, the effect of the action of segmentation so as to effect a readjustment according to the Leuckart-Spencer principle, is to bring about discontinuity of growth or reproduction through fission.

8. The asexual method of reproduction seems to have been purely a consequence of the operation of forces under the laws of cumulative integration and the law of Leuckart and Spencer, under varying conditions, and to have led to a continuously repeated division of living matter, as fast as it was formed into small masses, through direct processes of fission, composed at first almost wholly of nucleoplasm or chromatin.

9. As cytoplasm began to be developed more abundantly there seems to have been developed a tendency for the products of segmentation to cohere. We may therefore distinguish very sharply these two kinds of segmentation as *disruptive* and *coherent.* But the greater development of cytoplasm was itself a consequence of cumulative integration, which proceeded so fast that its products could not be converted into nucleoplasm or chromatin with sufficient rapidity so as to be in a condition to fall apart as small cells as a consequence of the action of the direct process of fission. The evidence for this is the fact that the nucleoplasm or chromatin, in higher forms, is derived by constructive metabolism from cytoplasm and is the end-product of the latter.

10. The secondary evolution of a cytoplasmic field led to a process of divergent evolution or in the production of two kinds of cells, the most primitive or ancestral of which was poorly provided with cytoplasm, while the secondary form was provided with a thick cytoplasmic envelope.

11. The primitive minute form of cell is to be identified as the asexual one, which afterwards became "male," while the large overgrown type of cell, loaded with cytoplasm and its secondary products, is to be identified as "female" or as a cell on the way towards disruption into male cells, which tendency it still betrays in the process of extrusion of polar bodies. The arrest of this process of fragmentation in the case of such large cells loaded with cytoplasm, led to the evolution of the ovum from the spermatogonium or such a cell as was primarily destined to produce male cells as a result of its further fission.

12. The male state is therefore the primitive one, and in the prodigious fertility of the male represents the primordial, asexual, flagellate types. The female cell is a secondary and derived form developed after a cytoplasmic field has been evolved and after cell-aggregates began to become coherent.

13. This differentiation was primarily due to cumulative integration, or assimilation beyond the current needs of the organism; the female cells to which this overgrowth was diverted have tended to grow far beyond the average dimensions of the other cells of the body of the parent, and this excessive size is proof that they have in some way lost the power to undergo spontaneous segmentation, except in the case of parthenogenesis. Cumulative integration is consequently responsible for the evolution of the asexual, sexual and parthenogenetic modes of reproduction.

14. Ovarian egg and spermatozoön are not homologous; ova after extrusion of polar bodies are the homologues of spermatozoa. Ovarian ova and spermatogonia are, in many cases, exactly homologous.

15. The expulsion of the polar bodies and detachment of the egg from the parent exhaust its power of continued spontaneous growth except in case of parthenogenesis.

16. The male cell as a consequence of the reduction of its cytoplasmic field at last became incapable of further independent development.

17. The male and female elements became reciprocally attractive to one another (sometimes through the production of certain chemical substances in the vicinity, Pfeffer), and in that their idioplasm is less different from one another than that of other cells there is no bar to their fusion, which is also favored by the fact that in the male cell with its preponderant chromatin there is now an attraction or need developed for more cytoplasm similar to its own diminished quantity, while conversely there is a similar need or attraction developed in the egg for additional chromatin in consequence of its preponderating cytoplasm. This leads to the highest form of cumulative integration through direct fusion of the male and female elements, or what I shall call reciprocal integration without loss of molecular identity, or as it is commonly called, to "fertilization." "Fertilization" is a reciprocal restoration of the equilibrium between the chromatin or nucleoplasm and the cytoplasm of both ovum and spermatozoön, this takes place not with accompanying molecular disintegration but by the actual fusion of both elements without the sacrifice of the molecular identity of either. Mutual digestion is not possible, for both elements are already composed of similar molecules. This molecular similarity constitutes the means through which the hereditary traits and tendencies of the male and female are transmitted.

18. The accumulation of cytoplasm in the egg through cumulative integration has enlarged its cytoplasmic field beyond that of any cell of the parent body. The result is that when "fertilization" occurs or fusion with the male cell, a series of segmentations are set up in this mass which are independent, and under the influence of new conditions, lead to the continuation of growth as the development of an embryo. This development is rendered directly possible only in virtue of the fact that there is a large cytoplasmic field in which nuclear motion and growth can take place in three dimensions temporarily without access of nutriment, while the resulting segmentations are coherent and tend to take place in such order and relation as to produce a being similar to the parent. The aggregation of large masses of segmentable plasma through the operation of cumulative and reciprocal integration has enabled the products of such simultaneous and successive segmentations to cohere and remain a multicellular aggregate, and to lay the foundation and become the direct cause of all metazoan and metaphytic organization.

19. The augmentation of the mass of the egg through cumulative integration and the development of the oösperm through reciprocal integration, has rendered possible the development of embryos without need of other nutriment during the preliminary or larval stages of ontogeny, thus leading also to the evolution of all larval forms, through processes of direct adaptation.

20. The achievement of the multicellular condition is probably to be

traced to the secondary evolution of a cytoplasmic field, sexuality also having so arisen at about the same time. The multicellular or coherent condition produced new and more complex morphological relations leading to the manifold differentiation of physiological functions in relation to diversification of surroundings, thus introducing a new and powerful cause or capacity for variations and adaptations under such diverse conditions. It is in the highest degree probable that the evolution of a cytoplasmic field and of sexuality, which depends upon the former, first rendered variability possible.

21. Cumulative integration in the vegetable led to the process of cumulative integration in the animal world and to the overproduction of germs or young in both of these kingdoms of life. The rate of increase thus became augmented in a geometrical ratio, as supposed upon the Darwinian hypothesis, which on the basis of the theory of the struggle for existence and the process of natural selection so evoked, accounts for the preservation through survival and inheritance of valuable or advantageous variations which first arose as supposed above. Cumulative integration is regarded as the primary cause of morphological differentiation under the stress of diverse conditions, as well as of the geometrical ratio of increase of individuals and consequently of the struggle for existence. The effects of the struggle for existence have however been modified through the already attained morphological differentiation of many forms in that the nature of further possible modifications have been in some cases very clearly determined by the character of those which have immediately preceded the last modification. This principle of cumulative adjustment through which superposition of adaptations occurs, is the law of cumulative morphological differentiation.

22. The only cells in multicellular forms which are absolutely otherwise functionless are the germ-cells. They alone, therefore, can become the vehicles for the transmission of all the traits of the parent in higher forms. They are the only cells of the body which, by any stretch of the imagination, can be supposed to possess the recapitulative power manifested in ontogeny.

23. In that the germinal cells are never belabored with any physiological function in the parent body, except cumulative integration, they are also the only ones which lead the charmed life of a perpetual youth. Upon this peculiarity of germ-cells depends rejuvenescence through reproduction, and the maintenance of the maximum vigor of the species.

24. In that maximum vigor of growth concentrated upon apical or nearly acropetal cells in plants determines their sex, and in that this seems to hold in great measure in Algæ and Fungi, and in that the gradually deeper inclusion of germ-cells and germ-tracts in animals is clearly a consequence partly of further morphological development, as well as of the effect of the repulsion of the functionless germ-cells into positions where

they are out of the way of interference with the exercise of the functions of the rest of the cells of the body, we have some clews to the reason why germ-cells are "set aside," not as the consequence of a *foreseen* (by the organism or natural selection) necessity for their isolation, *a la Weismann*, but as a consequence of the continuous action of cumulative integration ending in continuous growth, sexuality, morphological and physiological differentiation under the stress of surrounding conditions to which adaptive responses must as continuously be made.

25. With the evolution of the multicellular condition and sexuality, through cumulative integration, sexual correlations and interdependences between plants, insects and air-currents were evolved, as supposed in the text, while in animals sexual passion was evolved in the progress of sexual evolution. These factors became the motive forces which sustained the process of reciprocal integration or fertilization at its maximum of efficiency, and thus provided for the continuous rejuvenescence of living forms.

26. "Maternal" and "paternal" are relative terms. There was a time when asexual reproduction, through fission without karyokinesis, was effected by forms which were morphologically male. When individuals became developed in which the physiological functions of the individual were so adjusted automatically through a correlation of those functions as to impede the production of chromatin or nucleoplasm, presumably through the too rapid action of cumulative integration, cytoplasm was produced in a preponderating measure, the spermatogonia were hypertrophied and discharged before complete maturation as ova. In this way femaleness arose, and as "sex" thus became reflected in the physiological tendencies of the individuals of a species, some became male and others female. This carried the principle of the physiological division of labor beyond organs and extended it to individuals of the same species. The female, let me repeat, is a repressed male state.

27. In the production of female germs (ova, oöspheres) there occurs a prolonged process of integration of plasma so as to increase the volume of the cell-body, under conditions different from those obtaining in the production of male elements. In the production of male elements (spermatozoa, antherozoids), on the contrary, an actual process of elimination of cytoplasm often occurs, so as to reduce the latter to a minimum, and leave little remaining except the nucleus and its chromatin. The modes of production of the male and female elements, therefore, stand in the most extreme contrast to each other. The male state, on account of its prodigious fertility and the flagellate type of its products, is to be regarded as a reversion to the asexual method of reproduction as respects the physiological methods involved and the morphological character of the elements produced.

28. Reciprocal integration or sexual conjugation, otherwise "fertiliza-

tion," is an asexual method of reproduction superimposed or blended with another in which the last evolved sexual element has been hypertrophied as an ovum. The exhaustion of the central controlling mass of nucleoplasm or chromatin after expulsion of the polar bodies, together with the great size of the egg, has rendered it passive. The recurrence of the minute flagellate condition as "male" has rendered the male element active.

29. Male and female "sexual" products were at first and still continue to be dehisced as useless products of overassimilation or as a consequence of the cumulative action of integration, after further recapitulative growth in the form of new axes or individuals, growing in organic union, as in colonial organisms, became impossible, due to crowding, the culmination of seasonal growth or the morphological specialization leading to definite or constant formal individuality.

30. The "setting aside" of germ plasma must therefore be attributed to the direct action of cumulative integration, and cannot logically be considered as a "device" through which the immortality-isolation of germinal matter was to be achieved as a purpose or end.

31. Continuity of growth as continuously maintained through the physical capacity for living matter to increase its mass, was the primary factor in divergent evolution. The first step which it effected in adaptation was the necessity for segmentation either with or without karyokinesis, according to the law of Leuckart and Spencer. As soon as coherent, successive segmentations became possible, the first stage of which is seen in *Volvox*, the first step of morphological differentiation also conformed directly to the requirements of external conditions in that a blastula form was assumed which gave the maximum of surface in combination with the simplest form of coherence which could be developed through successive and simultaneous coherent processes of cleavage.

32. Sexuality, parthenogenesis, the extrusion of the polar bodies, larval development and the direct divergence of all higher types from the oösperm, are some of the effects of continuous growth as caused by continuous cumulative integration working under diverse conditions and the capacity to make direct adaptive responses.

33. The available evidence tends to show that sex is not predetermined in the egg, but is dependent upon internal conditions and correlations of metabolic activity within an embryo, so that sex may very often be influenced directly by the regulation of the food-supply long after development has begun.

34. The polar bodies are a phylogenetic reminiscence of the asexual or male flagellate state. There is not the slightest evidence to show that they are other than one of the manifold effects of continuous growth impelled to proceed as supposed above. They can certainly not be identified

as a "device" intended to prevent parthenogenesis, as supposed by Balfour, nor is it established that one of them is extruded "ovogenetic" plasma, while the other is *conveniently* extruded to save Weismann's ancestral germ plasma from molecular disintegration!

35. The divergence of type from the oösperm was determined by variations in the surrounding conditions, the effects of which could not be reflected upon the germinal matter set aside through the continuous action of cumulative integration, resulting in continuous growth, except through the action of the concurrent metabolism so affected. Metabolism under diverse conditions was therefore the only source through which the idioplasms of species could be developed, through which the continuity of the phenomena of inheritance is maintained.

36. The principle of continuous growth through cumulative integration, its rhythmical interruption through the "setting aside" and dehiscence of the useless sexual elements, the evolution of a cytoplasmic field, the direct adaptation to their surroundings of colonial aggregates of cells resulting from the coherent segmentation of masses of plasma resulting from reciprocal integration, the necessarily cumulative superimposition of adaptations upon one another, have been, in the main, the materials upon which natural selection was dependent in order to become operative in biological evolution.

37. The view that the female is preponderatingly "anabolic" and the male "katabolic," as held by Geddes and Thomson, cannot be sustained on the basis fact, since it is readily demonstrated that the male element represents a higher product of constructive metabolism than the female.

38. The most important result of the evolution of sexuality is the physiological process of nuclear substitution through reciprocal integration or "fertilization," thus blending and superposing matter and energy from two sources and causing the latter to be potentially stored. Hunger has brought about the material overflow, the divergence of the sexual elements from a common basis has ended in the production of countless adaptive modifications and the evolution of "species," while the accessory devices favorable to conjugation which have been slowly and adaptively evolved have led to a gradually intensified expression of passion and love, which have become important motive forces in the drama of evolution at large.